THE NORTH AMERICAN DISTRIBUTION OF THE GENUS *DRYOPTERIS*

Thomas M. Carlson
Division of Biological Sciences

W. H. Wagner, Jr.
Herbarium and Division of Biological Sciences
The University of Michigan
Ann Arbor, Michigan 48109

INTRODUCTION

The Woodferns, *Dryopteris*, are conspicuous, well collected ferns of mainly forests and swamps that occur over most of North America except the Great Plains. They become rare and sporadic in southwestern United States and in southern Florida. The 15 sexual taxa display a diverse array of mainly temperate, boreal, and arctic distribution patterns that appear to have been greatly influenced by Pleistocene glaciations. These patterns contribute toward an understanding of the complex phylogenetic relationships of these plants. There are nine diploid taxa and six polyploid taxa. Comparisons of possibly related Old World species provides insight into past distributions and migration patterns. Five of the polyploids are perhaps the most interesting in terms of glacial history; three of these grow exclusively in eastern North America. Glaciation may have played a major role in the origins of these allopolyploids by creating conditions conducive to hybridization. Two other allopolyploid Woodferns have amphi-Atlantic distributions, and Wagner (1971) proposed that they may have had a common parent (SS), now presumably extinct. As will be seen, similarities between the ranges of these two ferns support this suggestion.

The first comprehensive treatment of the overall geography of ferns was by Christ (1910). However, there are few in-depth studies (Smith, 1972; Tyron, 1969, 1970, 1971; Wagner & Wagner, 1965).

MATERIALS AND METHODS

The ranges are plotted of 13 of the 15 sexual taxa of *Dryopteris* occurring in North America, north of Mexico (including the two primarily Mexican taxa whose ranges barely extend into the southwest United States). Some of the distribution maps include localities in Iceland, a land mass often considered to be part of the Old World. The square symbols on the maps (Figs. 1, 3, 6, 8–19) represent herbarium specimens that we both examined and annotated. The dots represent localities learned from reliable literature or through correspondence with other pteridologists. Many of the specimens represented by dots were also seen by Wagner.

RESULTS

Dryopteris fragrans (L.) Schott (Fragrant fern) is a diploid that prefers shaded or exposed and usually north facing cliffs (Wherry, 1961; Carlson, 1979). Its
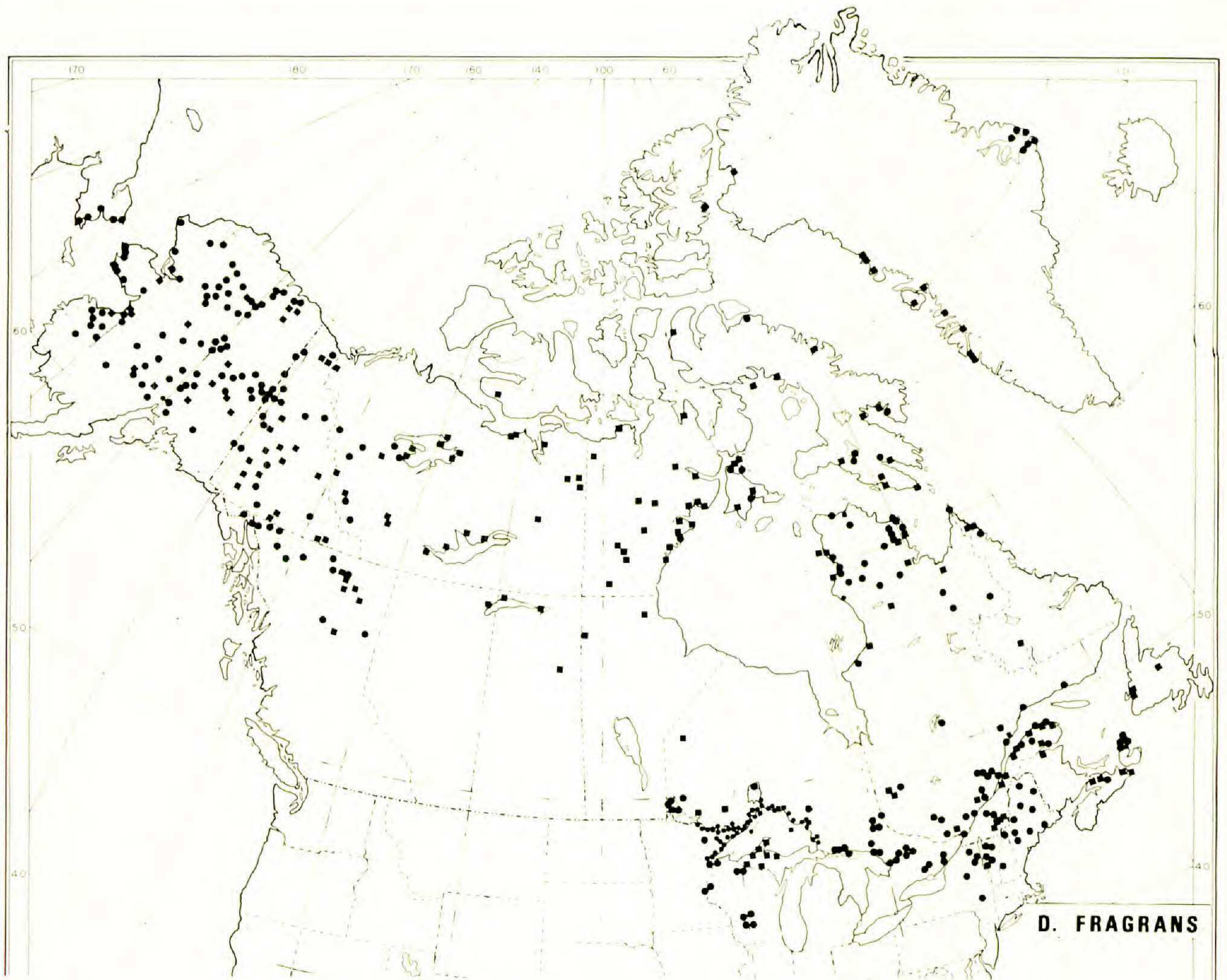
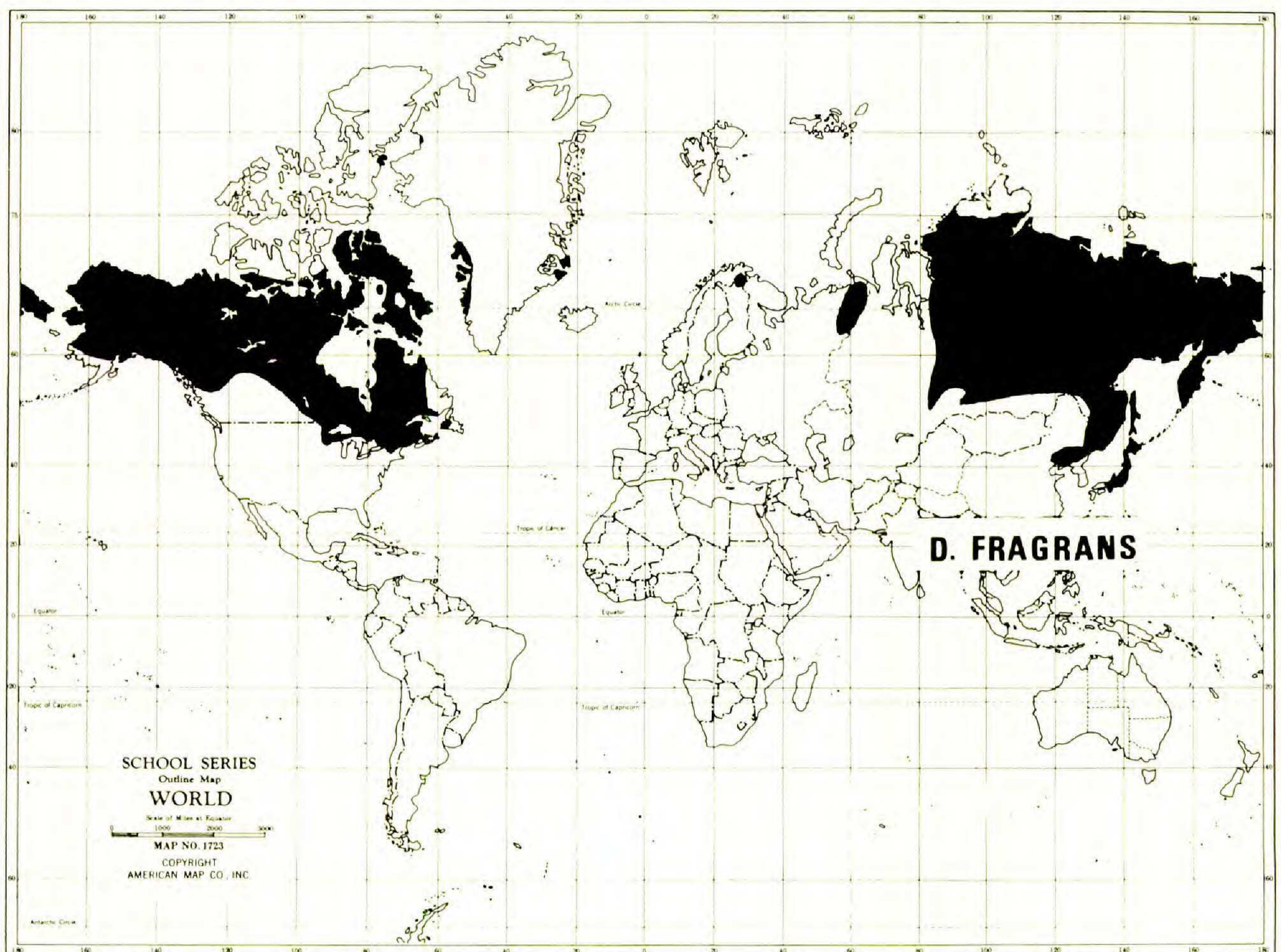FIG. 1. *Dryopteris fragrans* range in North America.

FIG. 2. *Dryopteris fragrans* approximate global range.

circumboreal-arctic range extends in northern latitudes through North America (Fig. 1) and across northern Asia and Siberia and southward into China, Korea, and Japan (Fig. 2), with disjunct populations in northern Finland and northwest Russia.

The circumboreal *Dryopteris filix-mas* (L.) Schott (male fern) is a tetrapoloid. Its taxonomy in North America is poorly understood. It may be an autopoly-
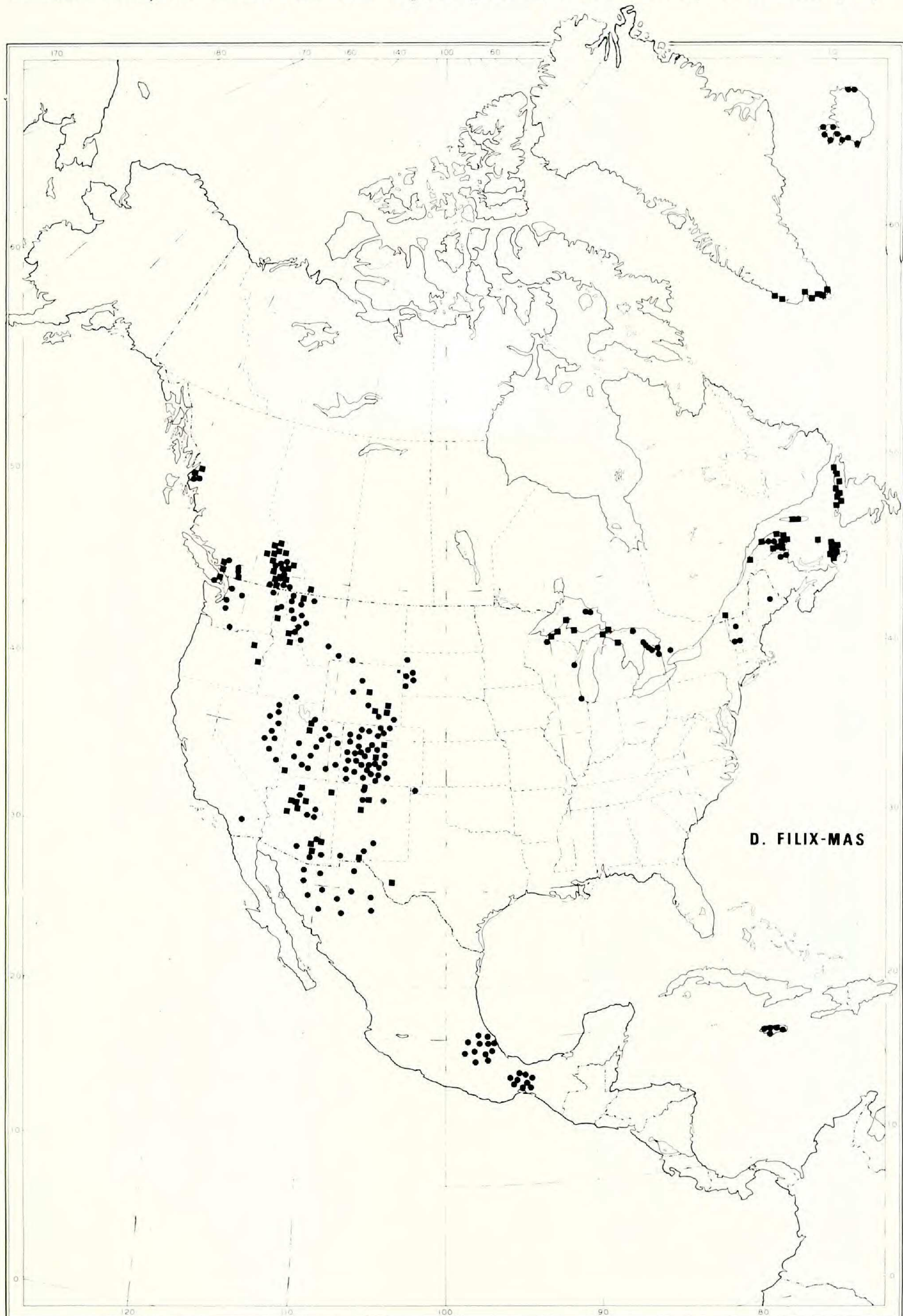

D. FILIX-MAS

FIG. 3. *Dryopteris filix-mas* range in North America.

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ploid (Wagner, 1971) or an allopolyploid (Britton, pers. comm.). It occurs in mountainous regions or in areas with exposed bedrock and/or talus slopes (Carlson, 1979) in most parts of its North American range (Fig. 3). In the west *D. filix-mas* extends through the Rocky Mountains from British Columbia to northern Mexico. Male fern also has a disjunct population in the San Bernadino Mountains in southern California. In eastern North America *D. filix-mas* is scattered from the Great Lakes to Greenland and Iceland.

Dryopteris arguta (Kaulf.) Watt (Coastal Woodfern), a diploid of rocky ravines and partially shaded slopes (Grillos, 1966), has a Cordilleron range extending along the west coast of North America from northern Baja Calfornia to southern British Columbia. It also has populations in the High Sierras of California as well as disjunct populations in the mountains of south-central Arizona in Pimal and Gila counties.

Jermy (*in litt.*, 1979) stated that when he examined specimens of this species from the University of California (Berkeley) herbarium, what appeared to be two distinct spore sizes were found. He suggested that the western American *D. arguta* may contain a tetraploid cytotype as well as the known diploid. Another variable character is broad and narrow frond forms. There are three frond types (narrow, normal and broad) (Fig.'s 4A, 4B, 4C). As illustrated (Fig. 5), the range of the narrow form is restricted to the High Sierras of California, while the broad form occurs on Santa Catalina and Santa Cruz Islands and along with one locality in Humboldt Co., California. The normal form grows predominantly along the coast but its range also overlaps with those of the narrow and broad forms. The two extreme forms may only be environmentally induced variations of *D. arguta* produced by local conditions.

Dryopteris expansa (Presl) Frazer-Jenkins (Spreading Woodfern), best known in previous botanical literature as *D. dilatata* (Hoffm.) Gray or *D. assimilis* S. Walker is a diploid of cool talus slopes and swamps, mainly in woodlands (Carlson, 1979). It exhibits an amphioceanic distribution pattern (Fig. 7) with populations in north temperate and sub-boreal eastern and western North America (Fig. 6), Europe, and eastern Asia.

Much confusion has existed regarding the North American range of Spreading Woodfern because it has been lumped with other species in the *D. carthusiana*
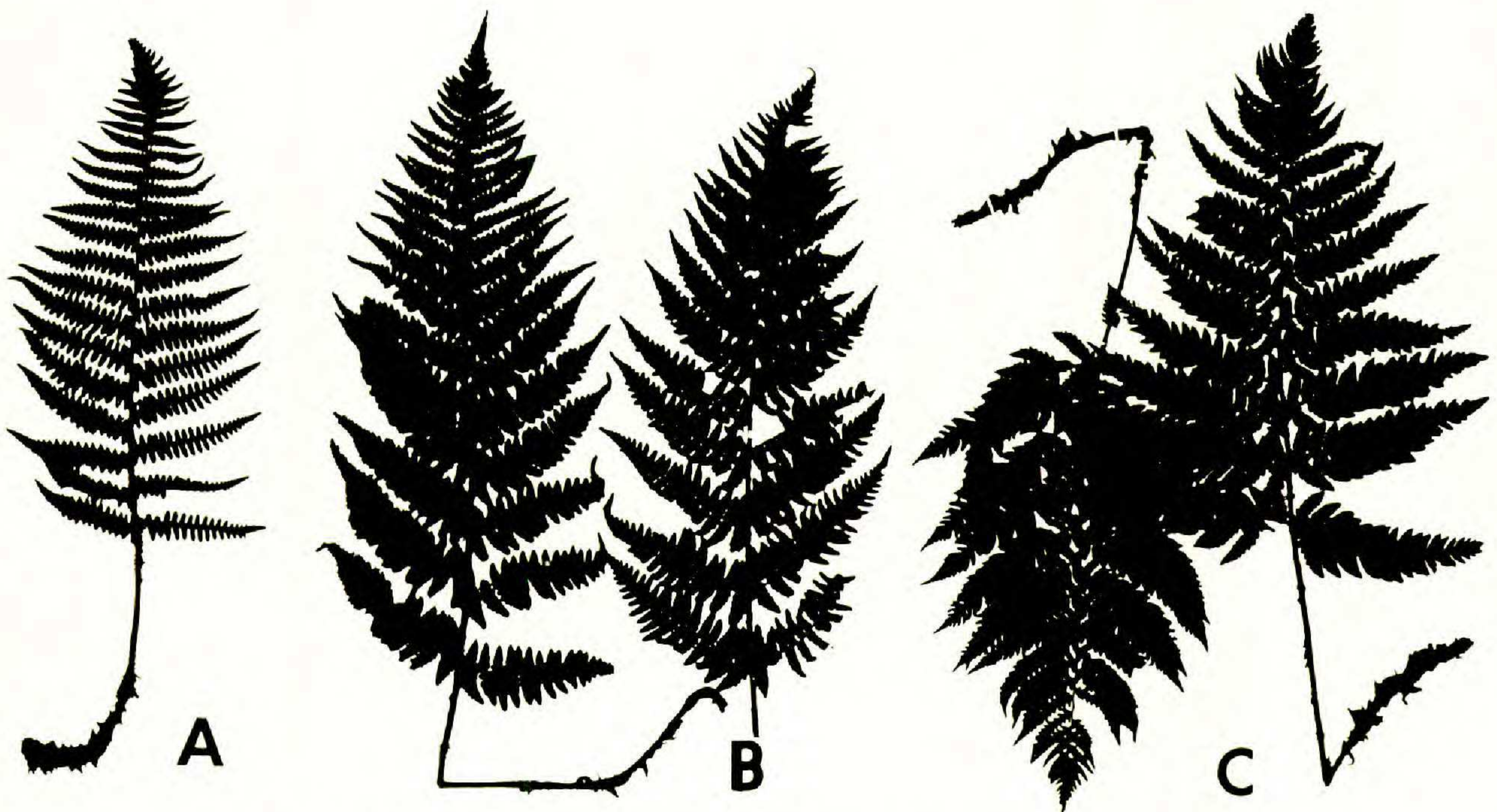

FIG. 4. *Dryopteris arguta*: silhouettes of herbarium specimens.

complex, which have collectively been called *D. austriaca* (Jacq.) Woynar (often also referred to as *D. dilatata*). For example, Hultén (1968) illustrated the range of *D. austriaca* as continuous between the Pacific and Atlantic oceans across Canada. However, careful examination and revision of western Canadian *Dryopteris* herbarium specimens an the subsequent mapping of their localities results in a pattern (Fig. 6) that supports Britton's (1972) suggestion that in western Canada the range of the Spreading Woodfern extends only as far east as western Alberta. *D. expansa* has also been confused with the allotetraploid *D. campyloptera* Clarkson (Mountain Woodfern) of eastern North America.
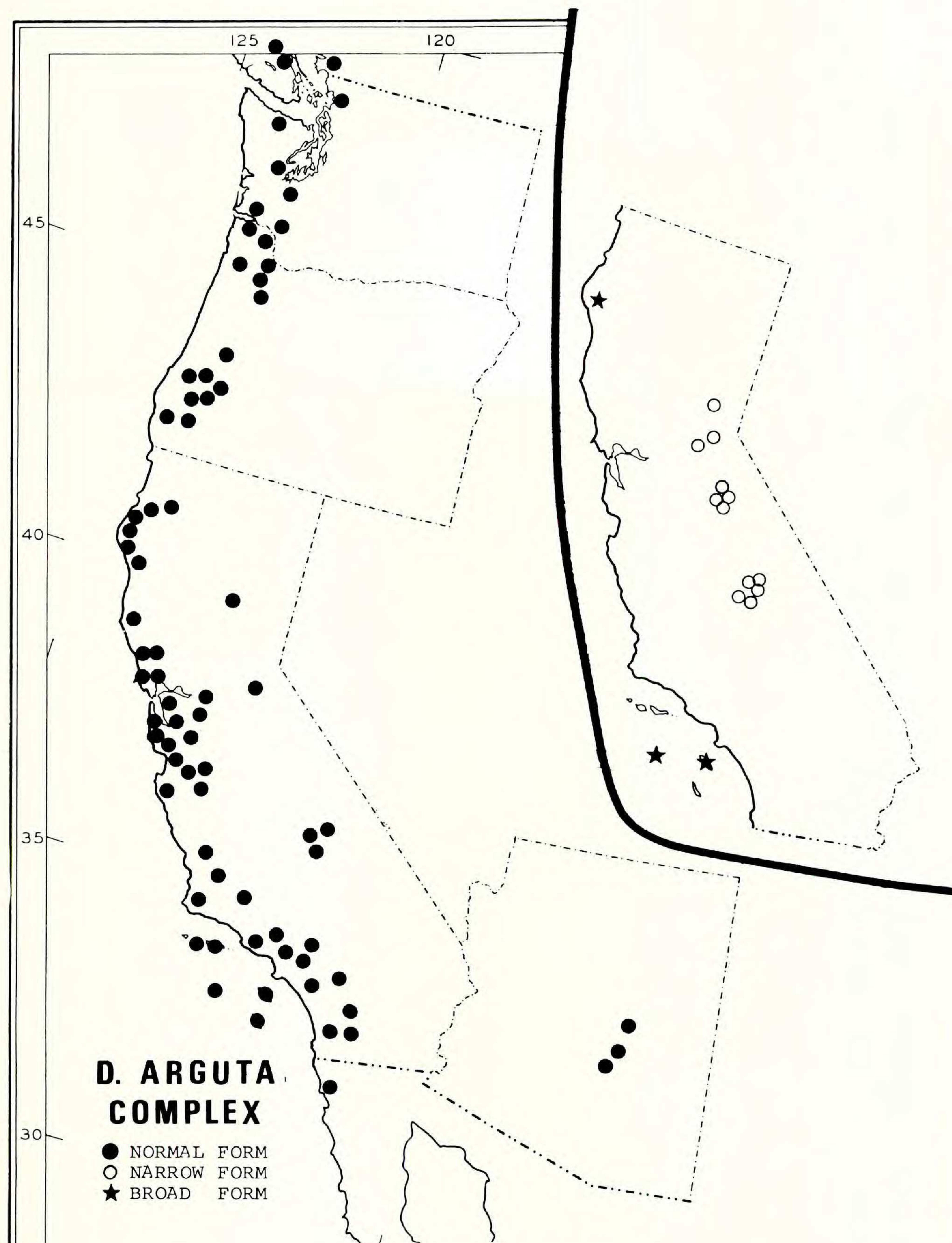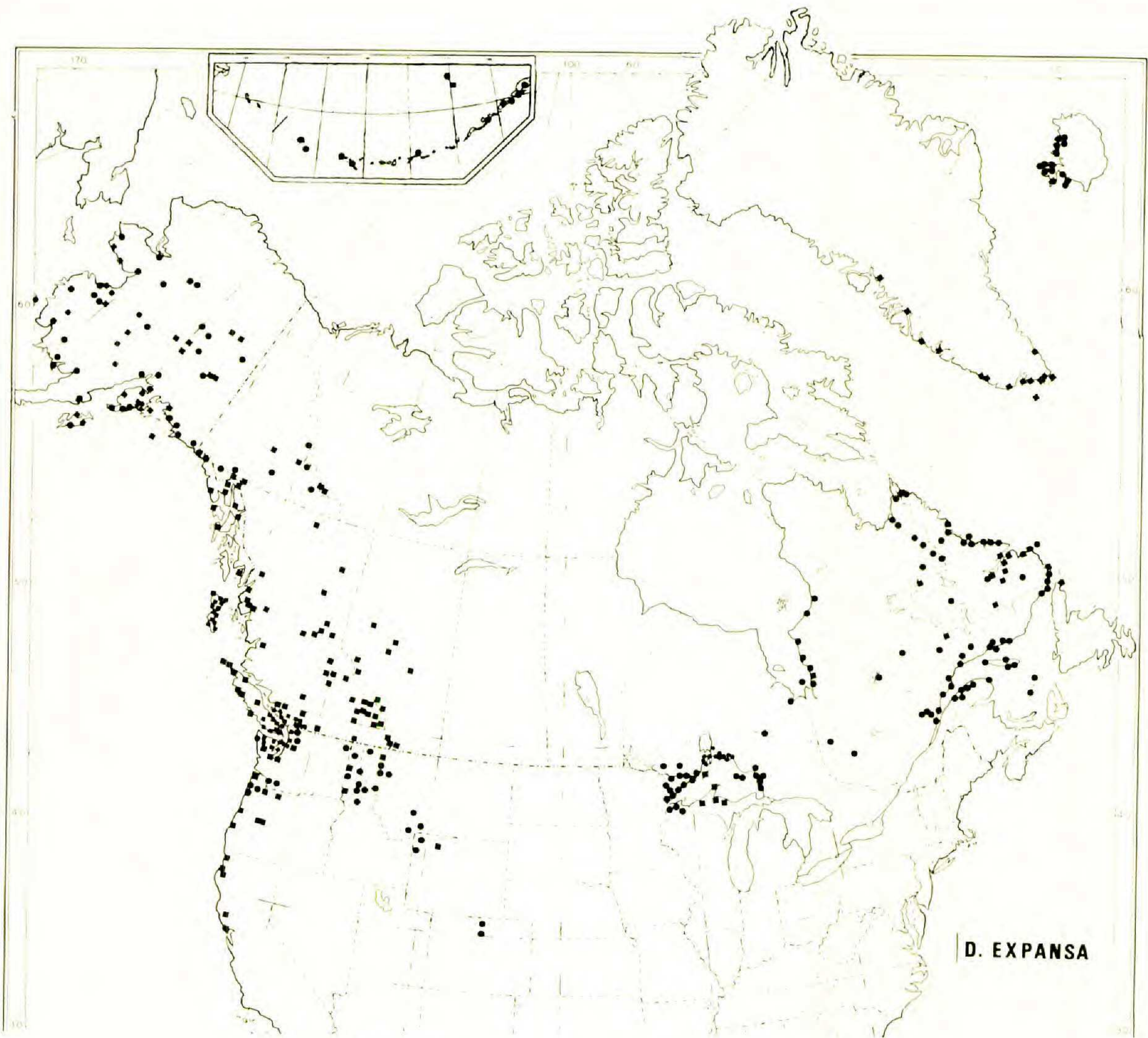

FIG. 5. *Dryopteris arguta* range.

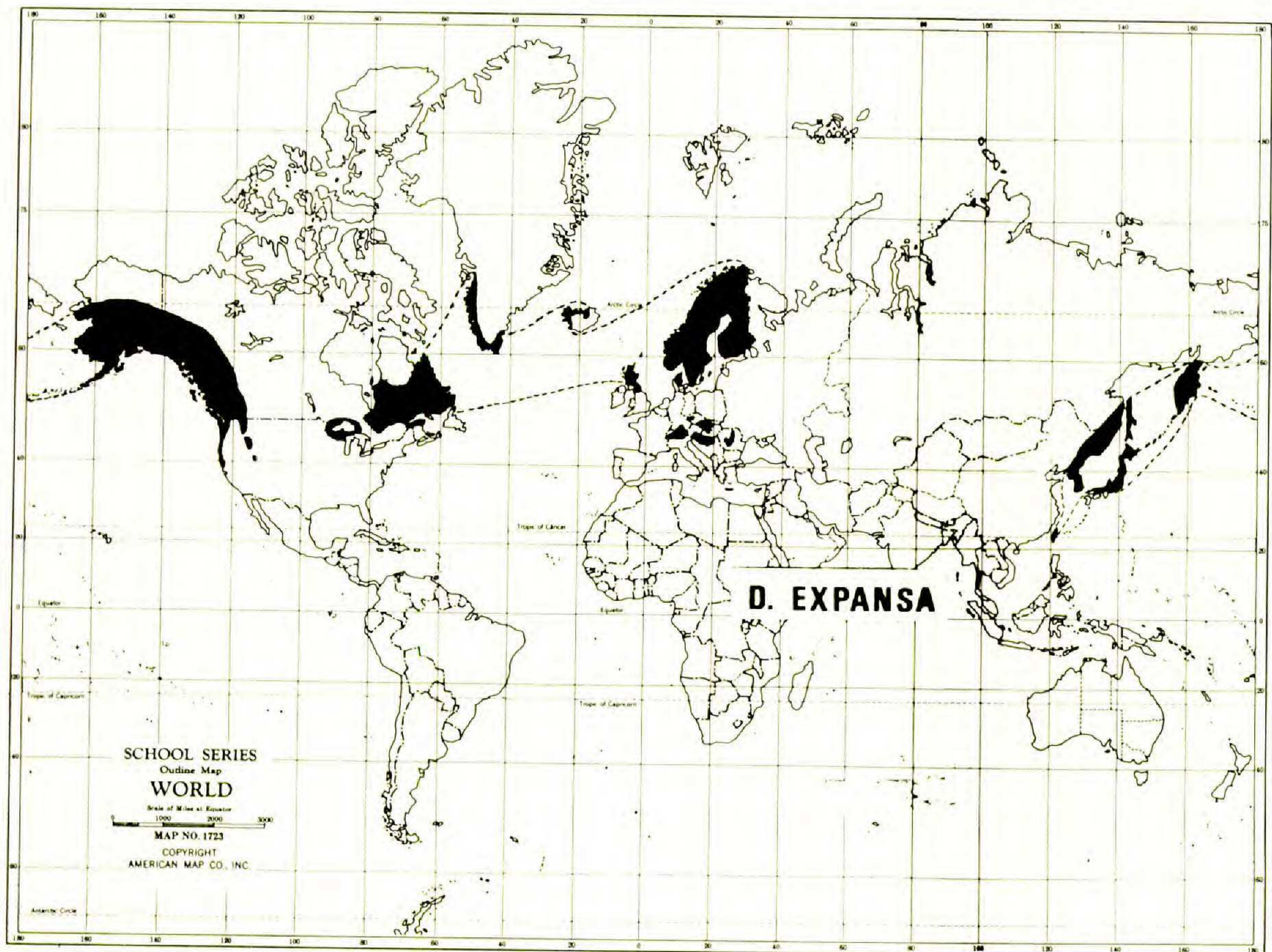FIG. 6. *Dryopteris expansa* range in North America.

FIG. 7. *Dryopteris expansa* approximate global range.

Four diploid Woodferns have ranges restricted to eastern North America. The two most common are *Dryopteris intermedia* (Muhl.) Gray (Glandular Woodfern, Florist Fern) and *D. marginalis* (L.) Gray (Marginal Woodfern). *D. intermedia* grows predominantly in rich woods while *D. marginalis* prefers drier more upland forests, particularly ones with rocky slopes (Wherry, 1961; Carlson, 1979). *D. intermedia* extends (Fig. 8) southward through the Appalachian Mountains into northern Georgia and Alabama and westward into eastern Missouri, central Iowa and northern Minnesota. In Canada it grows along the Great Lakes and the St. Lawrence Seaway, in Newfoundland, Nova Scotia, New Brunswick, southern Quebec and southeastern Ontario. The northern part of the range of *D. marginalis* (Fig. 9) is very similar to that of *D. intermedia* but it does not extend into Minnesota. However, the south Marginal Woodfern extends much farther west through the Plains states of Missouri, Arkansas, Nebraska and Oklahoma, perhaps because it tolerates drier habitats than does the Grandular Woodfern.

Dryopteris goldiana (Hooker) Gray (Goldie's Woodfern), a fern of extremely rich mesic woodland habitats (Wherry, 1961; Carlson, 1979), is another diploid Woodfern that is restricted to eastern North America, but it is considerably less common and its range (Fig. 10) is smaller than that of *D. intermedia* or *D. marginalis*, presumably because its habitat is much more specific. The southern bound-
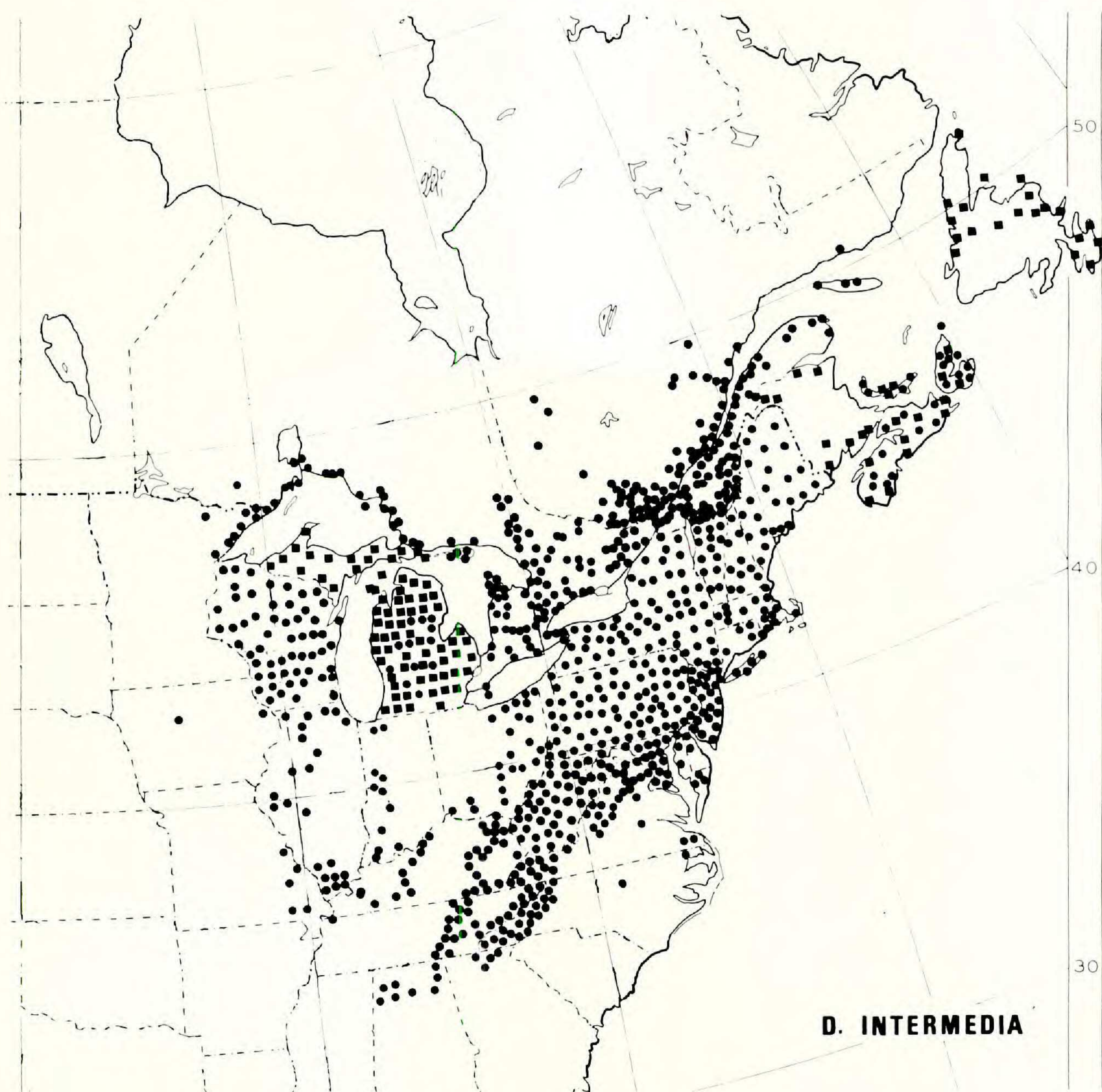

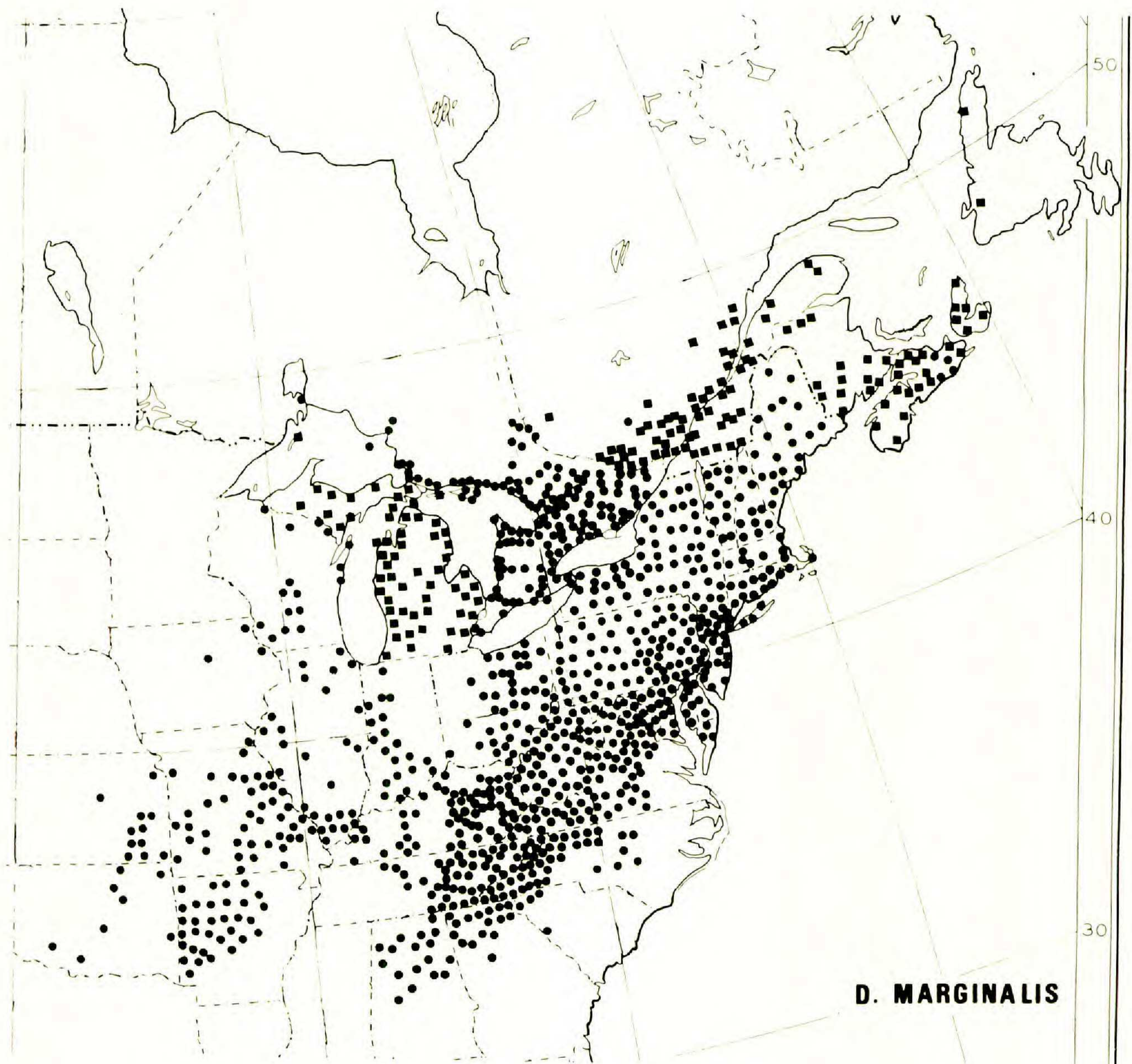FIG. 8. *Dryopteris intermedia* range.

FIG. 9. *Dryopteris marginalis* range.

aries of its range are similar to those of *D. intermedia* but it does not extend so far north; it reaches only southeast Ontario and southwest Quebec. *D. goldiana* does, however, extend farther west into Missouri than *D. intermedia*.

Dryopteris ludoviciana (Kze.) Small (Florida Woodfern), is a diploid whose distribution (Fig. 11) is restricted to damp woods and swamps and rocky ledges in hammocks (Wherry, 1972) on the coastal plain and the lower piedmont of the United States from North Carolina to Florida and west to Louisiana. It does however, extend up into the Cumberland plateau in Alabama.

Dryopteris celsa (Palmer) Small (*D. goldiana* × *ludoviciana*) (Log Fern) is an endemic allotetraploid which grows on rich hummocks and on rotting logs in swamps (Carlson, 1979). The present distribution of the Log Fern (Fig. 12) extends south from New Jersey to northern South Carolina and northern Alabama and west to northern Louisiana and western Arkansas. The range has two interesting disjunct areas, namely the vicinity of Rochester, New York region and southwestern Michigan. Disjunct populations of *Woodwardia areolata* (L.) Moore (Netted Chain-fern) and *Lygodium palmatum* (Bernh.) Sw. (Climbing Fern) are also known from southwestern Michigan. Several new localities for *D. celsa* have been found in recent years including additional localities in four southwestern Michigan counties, and a specimen from Missouri originally thought to be *D. clintoniana* (Eaton) Underwood (Clinton's Fern) was determined by us to be
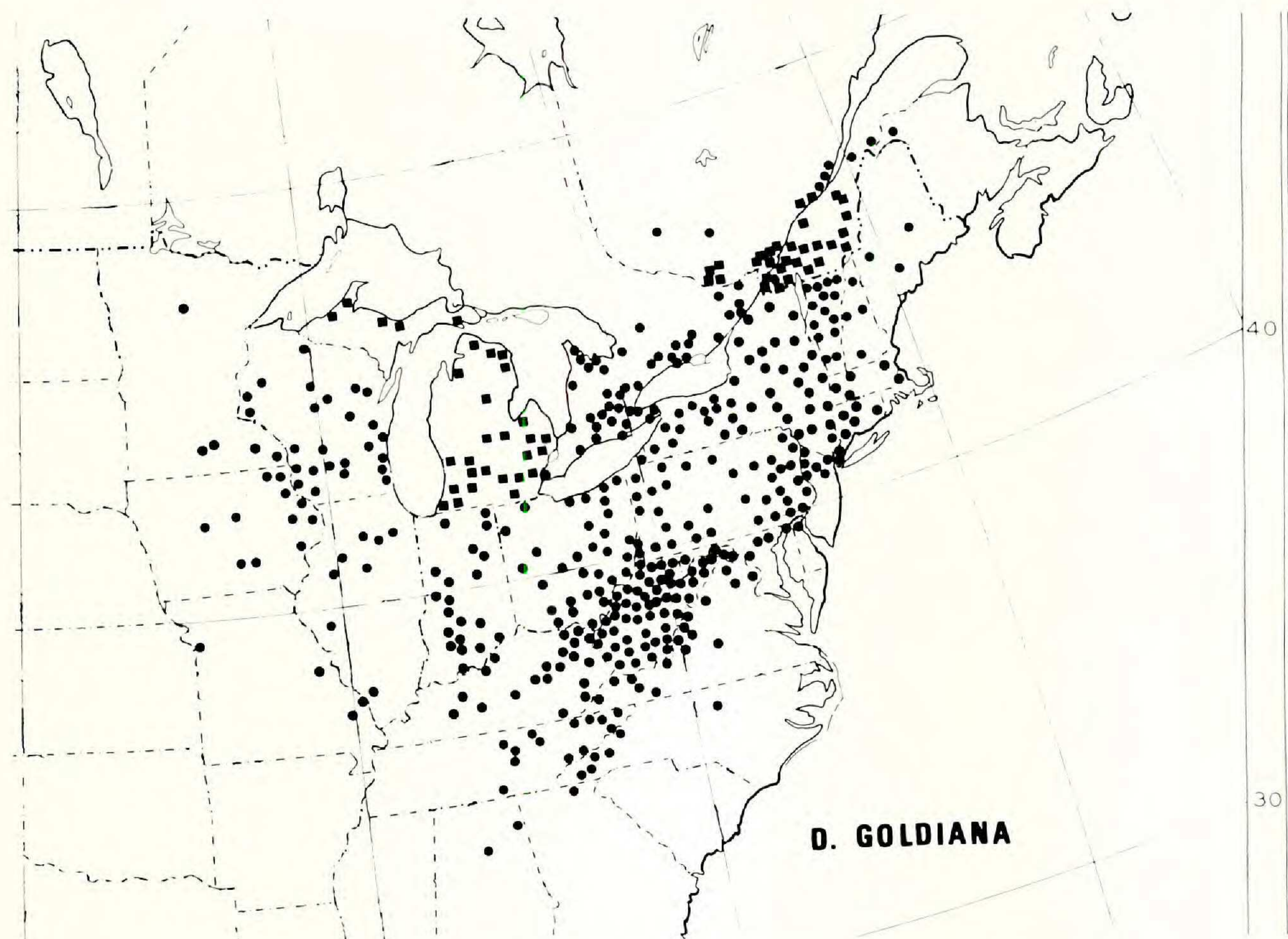
FIG. 10. *Dryopteris goldiana* range.
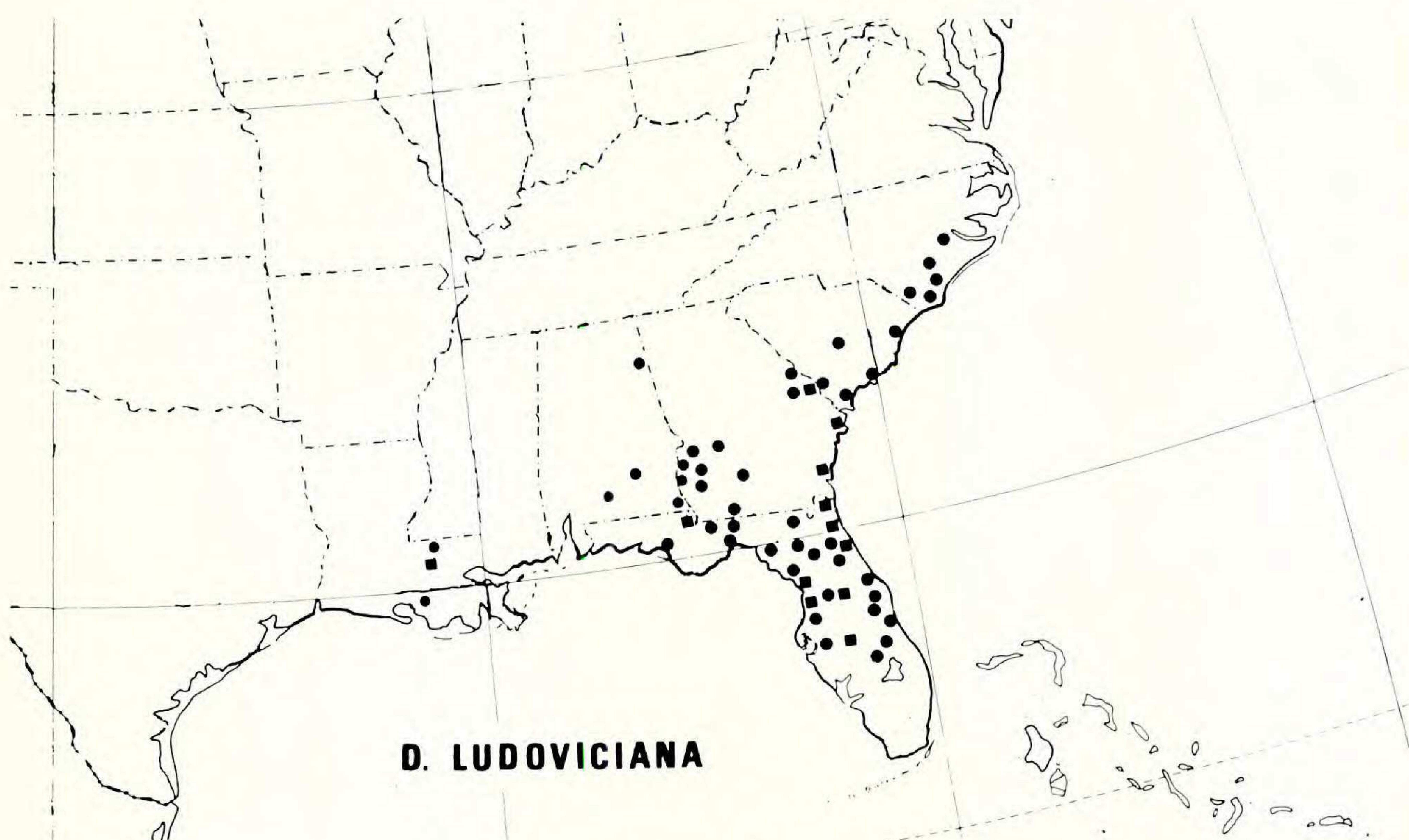
FIG. 11. *Dryopteris ludoviciana* range.

D. celsa. Single localities were also recently verified in both Illinois and Indiana, firsts for both states. Due to the morphological similarity between *D. celsa* and *D. clintoniana* 1, many *D. celsa* collections have been misidentified as *D. clintoniana.* As these mistakes are corrected, the known records of *D. celsa* may increase, particularly in the northern part of its range between its presently known disjunct populations and the major area of its assumed range.

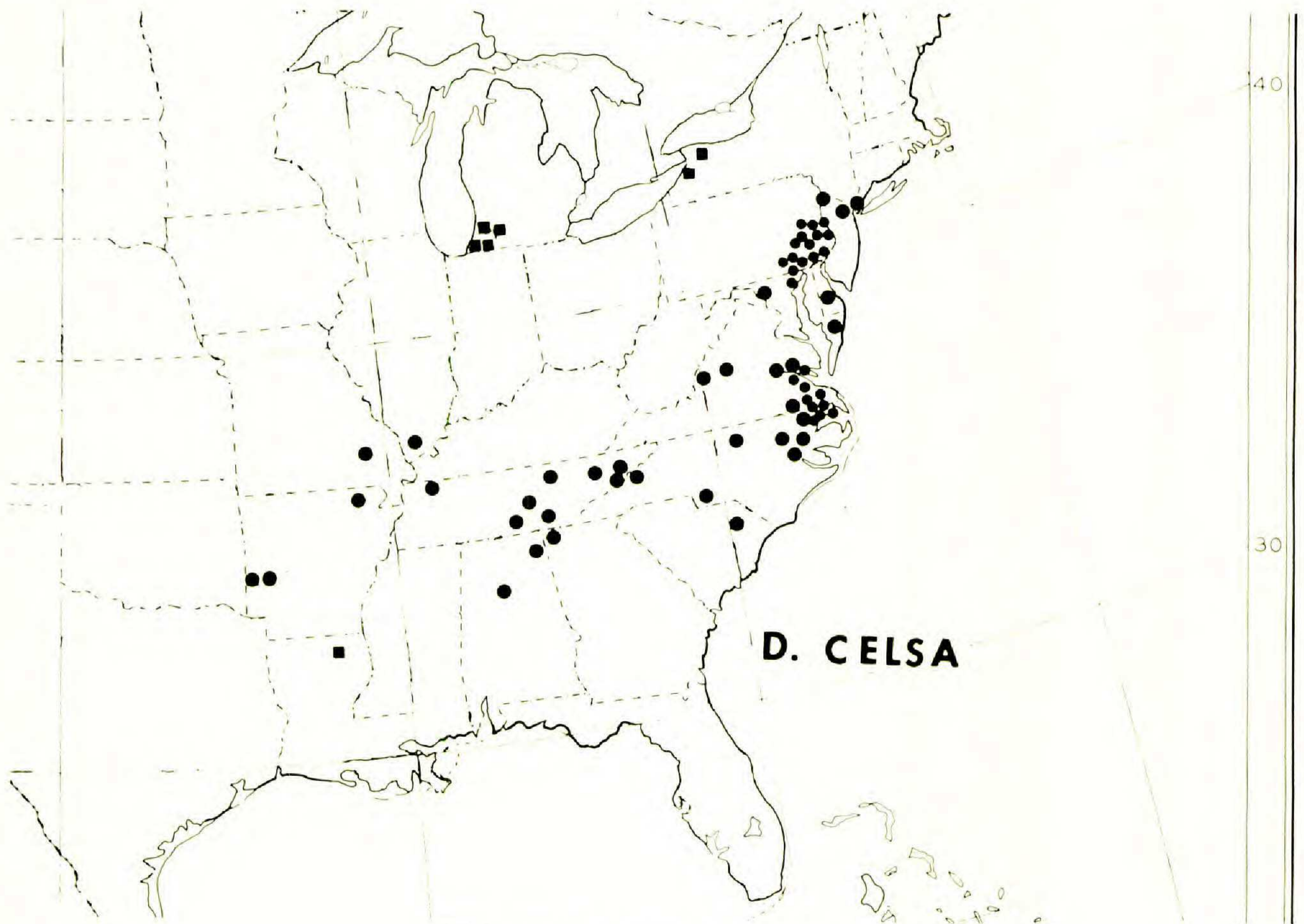FIG. 12. *Dryopteris celsa* range.

D. CELSA

D. GOLDIANA
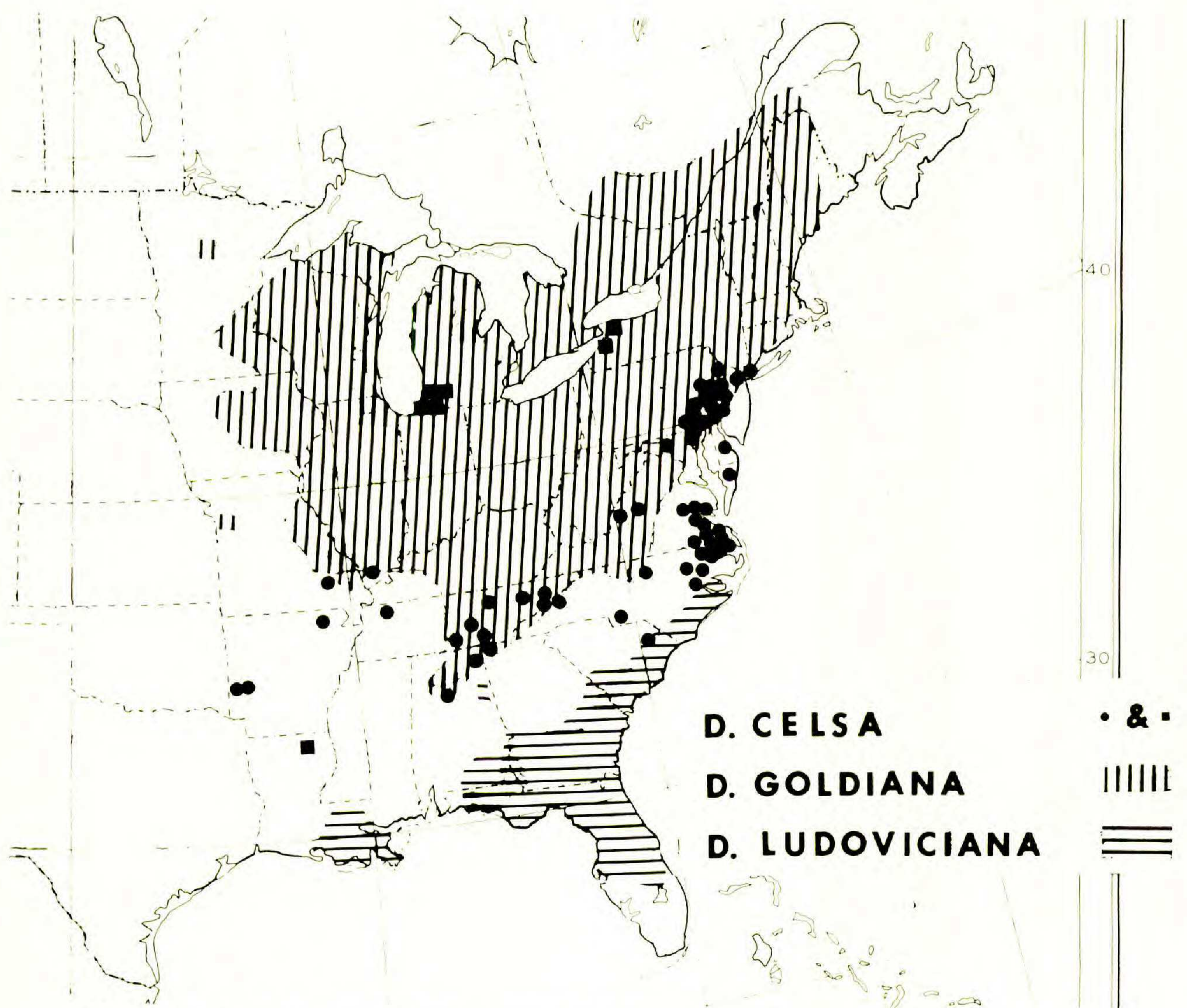
D. LUDOVICIANA

FIG. 13. *Dryopteris celsa* range with ranges of its parents (*D. goldiana* & *D. ludoviciana*).
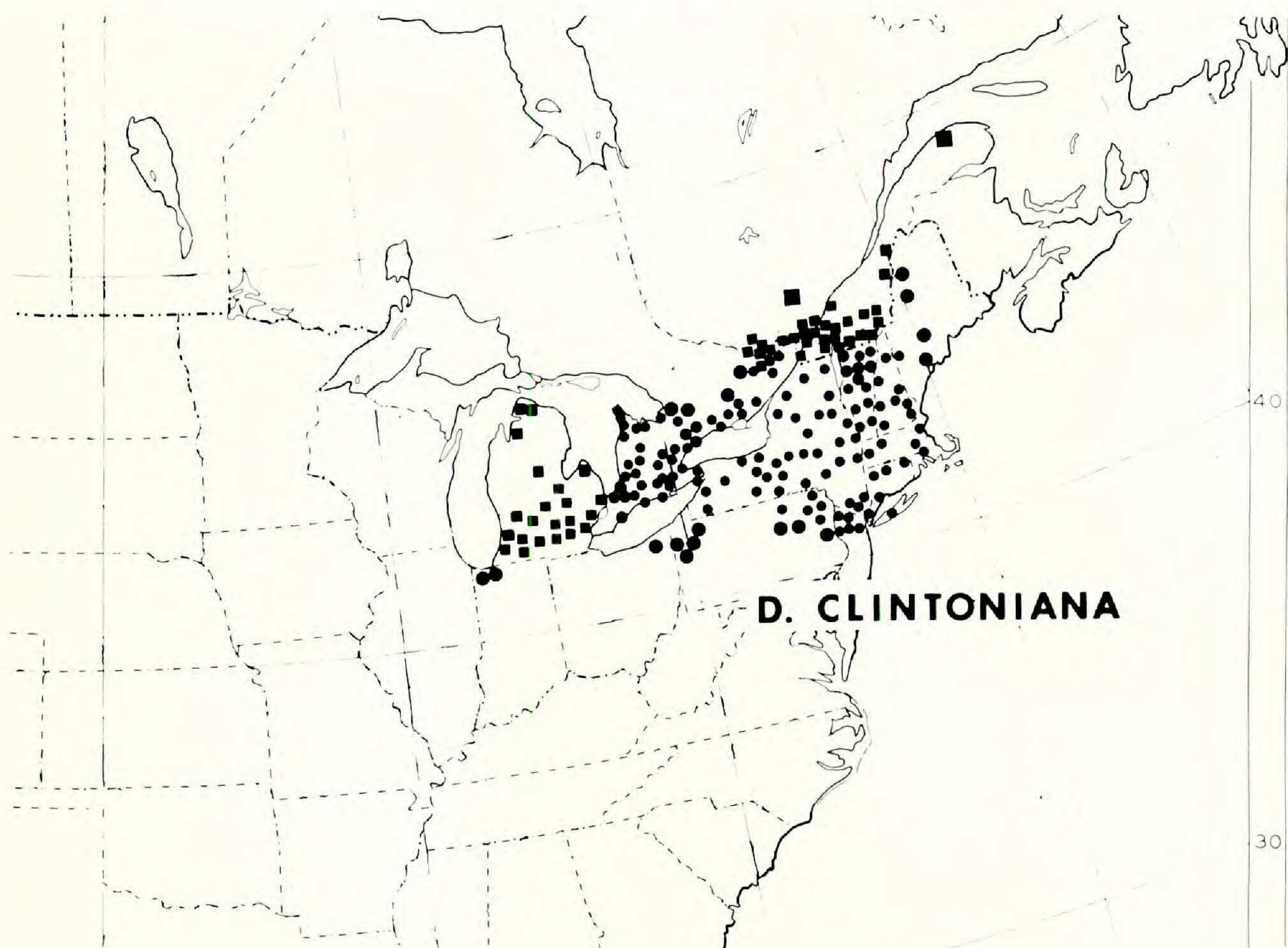
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FIG. 14. *Dryopteris clintoniana* range.
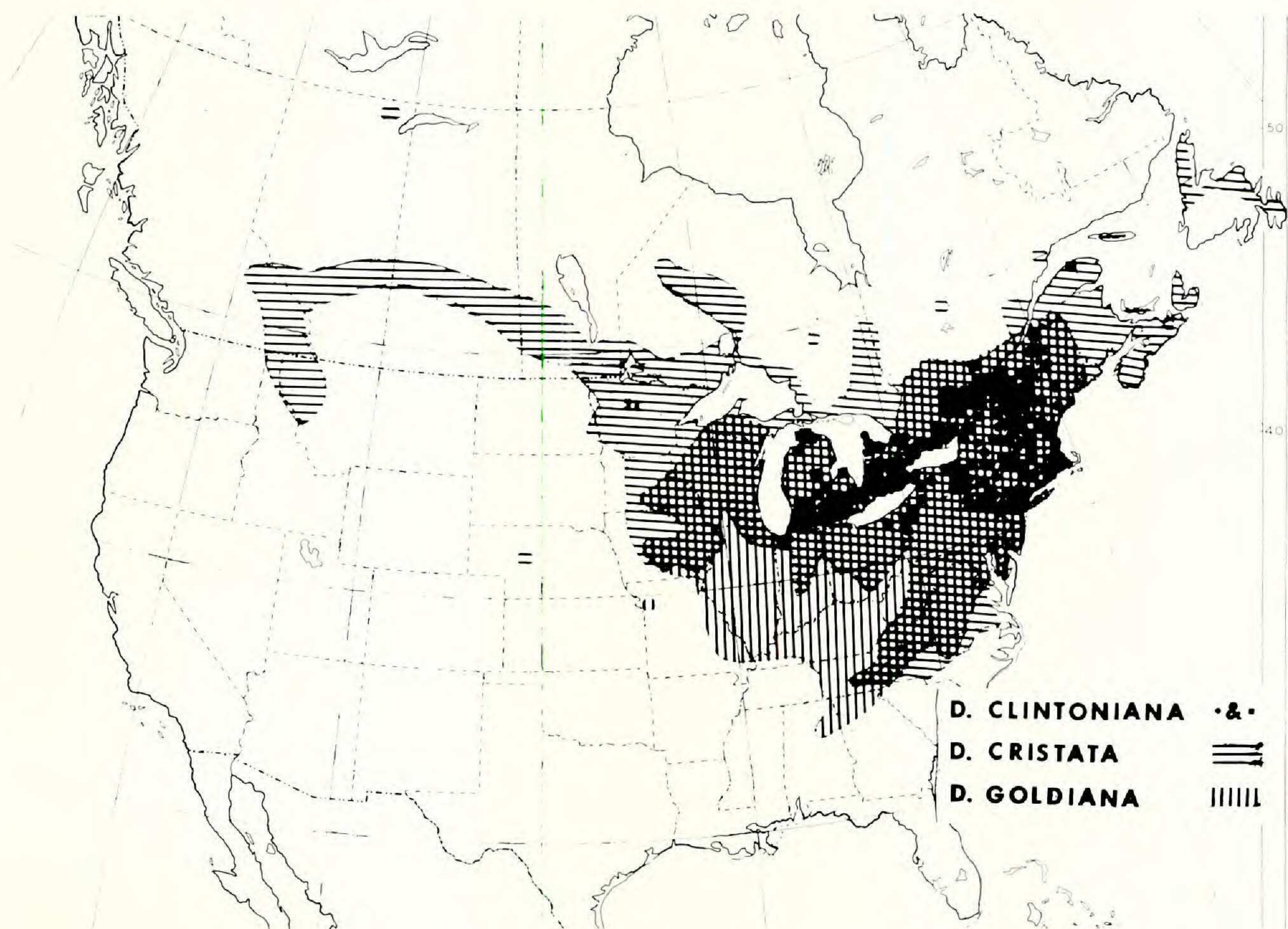
FIG. 15. *Dryopteris clintoniana* range with ranges of its parents (*D. cristata* & *D. goldiana*).

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These misidentifications have also led people to believe that the range of *Dryopteris clintoniana* (*D. cristana* × *goldiana*), a North American allohexaploid, extends much farther south than it actually does. Montgomery (1976) showed that in New Jersey *D. clintoniana* does not reach below the glacial border. The southern boundary of its range (Fig. 14) in Pennsylvania and New York also follows the southern boundary of the ice sheet advance. It has populations in northeast Ohio, northwest Indiana and much of the Lower Peninsula of Michigan. Its range in Canada is similar to that of one of its parents (*D. goldiana*) (Fig. 10) since it grows in [southern] southeast Ontario, [southern] southwest Quebec, in addition to a single known locality on the Gaspe Peninsula.
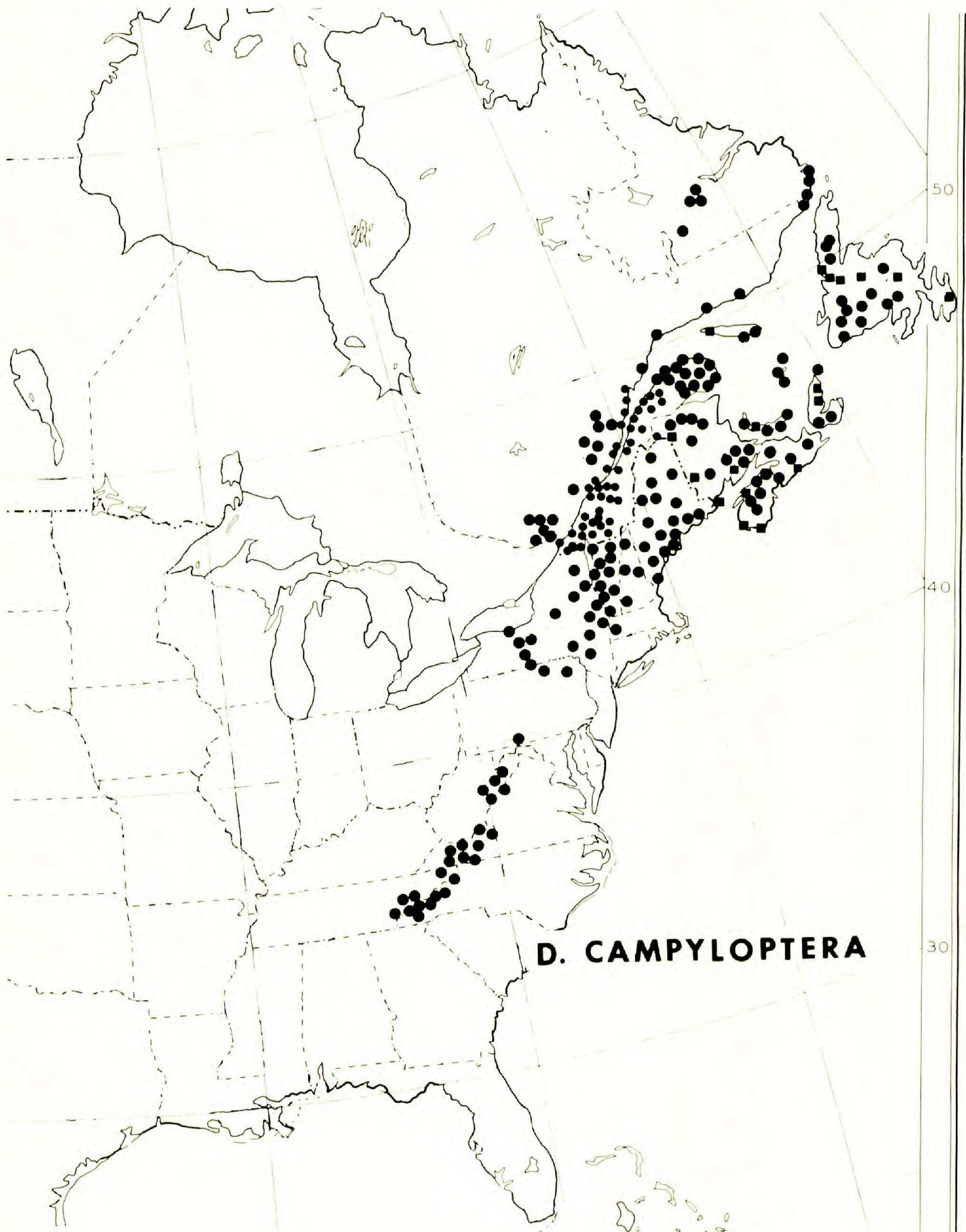
FIG. 16. *Dryopteris campyloptera* range.

   Dryopteris campyloptera is an endemic allotetraploid whose parents are *D. expansa* and *D. intermedia* (Wagner and Hagenah, 1962; Wagner, 1963; Wagner, 1971; Gibby, 1977). Its distribution (Fig. 16) extends into southeastern Canada as far north as Labrador and southward down the Appalachians through the United States to Tennessee and North Carolina.
   The two allotetraploid species, *Dryopteris cristata* (L.) Gray (Crested Woodfern) and *D. carthusiana* (Vill.) H. P. Fuchs (syn. *D. spinulosa* (Muell.) Watt) (Spinulose Woodfern) have amphi-Atlantic ranges. Because of their similar distributions, their ranges are described together. Both *D. cristata* and *D. carthusiana* are common throughout the Great Lakes region and in New England. Their ranges (Figs. 18 & 19) extend as far west as eastern North Dakota, and both have disjunct poulations in the same region in western Nebraska. The southern boundary of the range of *D. cristata* runs through southern Iowa, northern Illinois, southern Indiana and southern Ohio. In the Appalachians it occurs further south, being known from West Virginia, Virginia and North Carolina. The area of *D. carthusiana* extends south to northern Arkansas, southeastern Missouri, southern Illinois, Kentucky and northern South Carolina. Herbarium

FIG. 17. *Dryopteris campyloptera* range with ranges of its parents (*D. expansa* & *D. intermedia*).
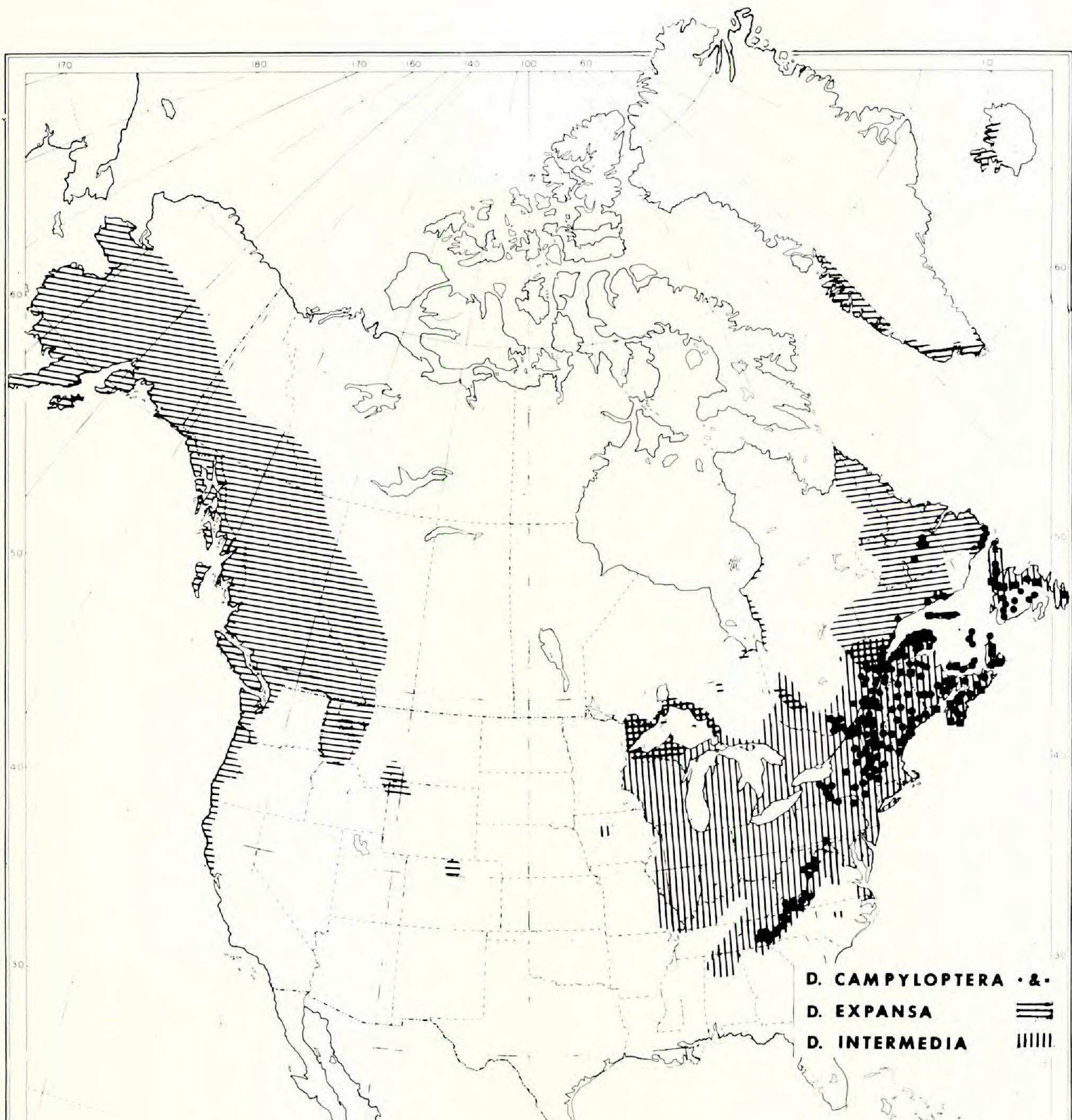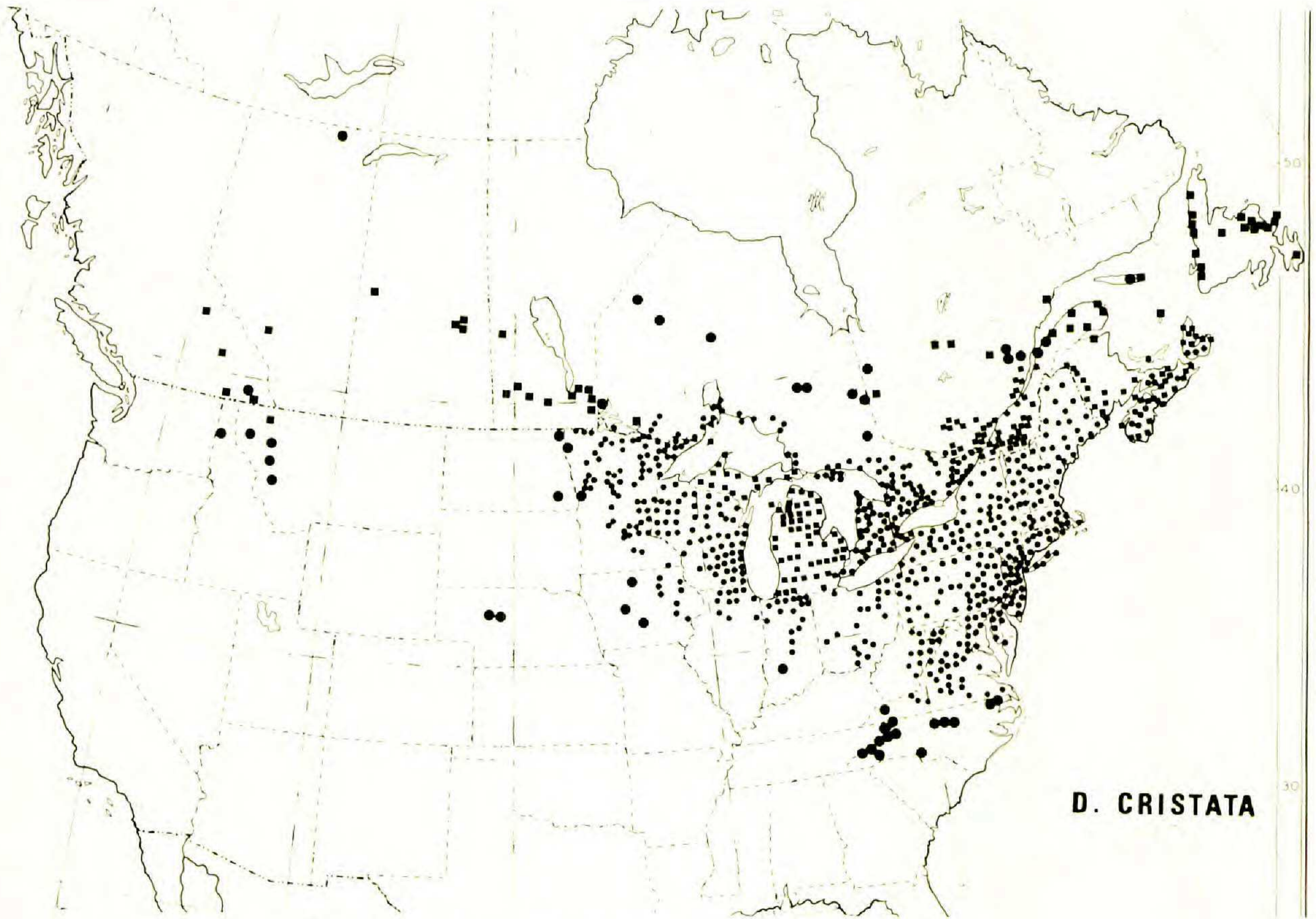
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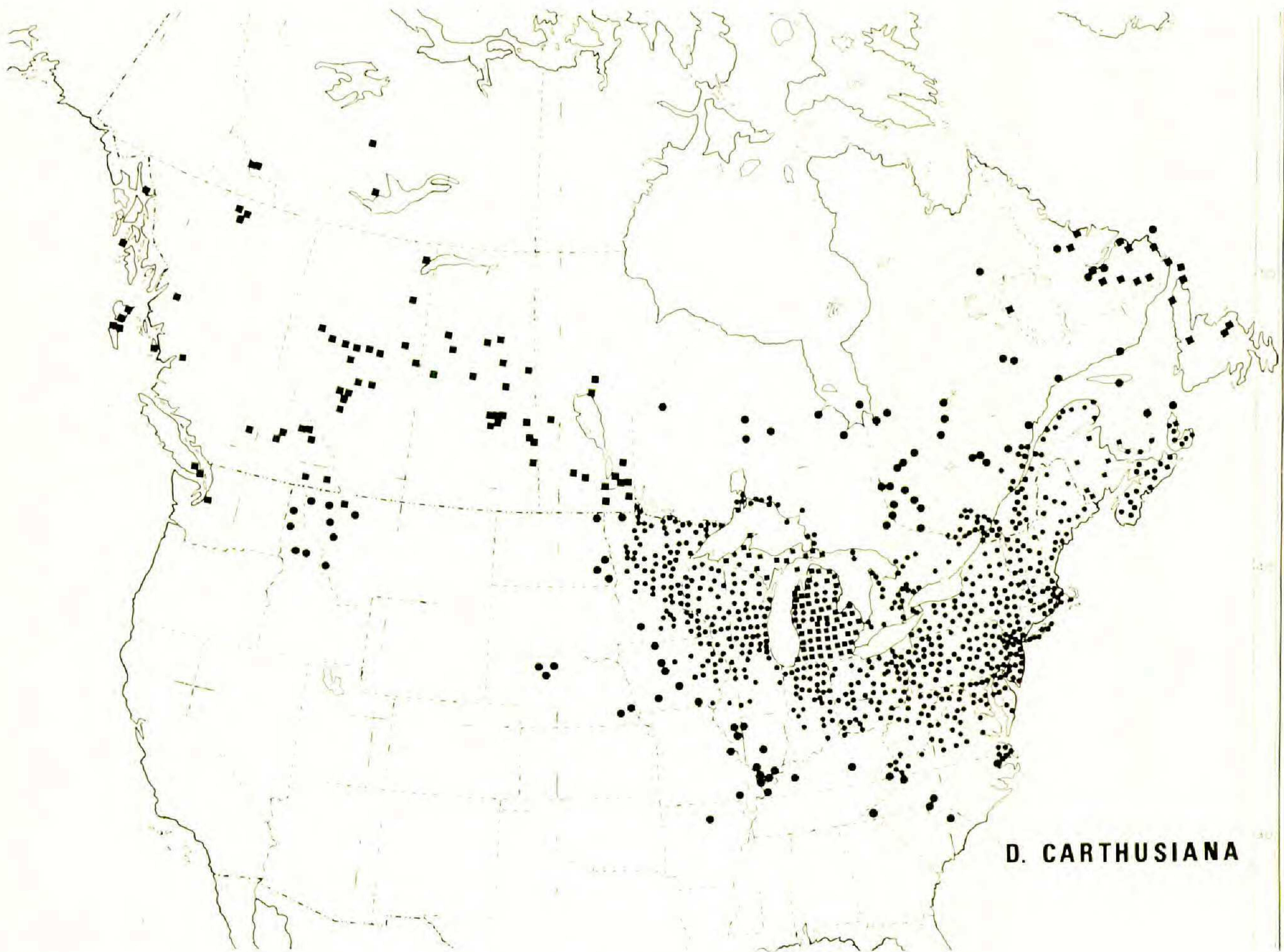FIG. 18. *Dryopteris cristata* range in North America.

FIG. 19. *Dryopteris carthusiana* range in North America.

specimens identified as both of these species are attributed to northern Alabama, but living populations are not known to us in this area.

In eastern Canada *D. cristata* grows as far north and east as Newfoundland while *D. carthusiana* ranges farther north through Labrador and Quebec. Both species extend westward across Canada to the Rocky Mountains. West of the northern Great Lakes the range of *D. cristata* constricts into a narrow band of scattered localities through southern portions of Manitoba, Saskatchewan and Alberta to the Rocky Mountains (southeast British Columbia, southwest Alberta, northern Idaho and northwest and west central Montana). *D. cristata* also has a disjunct locality near Lake Athabaska in northern Alberta. *D. carthusiana* likewise has a band of scattered localties running through the plains provinces but they are farther north than those of *D. cristata*. The range of *D. carthusiana* also reaches farther north in western Canada and farther west to the Pacific Coast extending as far north as Juneau, Alaska and as far south as Northwest Washington. Populations are also known in northern Idaho, northwest Montana and northward through Alberta and British Columbia in the Rocky Mountains to MacKenzie. In the Old World *D. cristata* grows mainly at middle latitudes in Europe with disjunct populations in central Russia (Fig. 20). *D. carthusiana* (Fig. 21) reaches farther eastward and northward in Europe. The eastern end of its range constricts into a narrow band which extends through middle latitudes of central Russia.

DISCUSSION

We here consider some of the major geological and climatological events to which the species have been exposed during their histories. The ranges of *D. expansa* (Fig. 6) and *D. filix-mas* (Fig. 3) have in common a gap between the Rocky Mountains and the Great Lakes region (with the exception of *D. filix-mas* populations in the Black Hills). Perhaps before the Pleistocene their ranges were continuous but during the glacial maxima they became discontinuous to the south of the ice and to the east and west of the Great Plains. Following the final retreat of the ice sheet the northward migration did not re-establish continuous ranges because of the vast open grasslands. These prairie habitats evidently exclude all *Dryopteris* species. At present some of the species (*D. intermedia, D. marginalis, D. goldiana, D. ludoviciana, D. celsa, D. clintoniana, D. campyloptera*) (Figs. 8–11, 12, 14, 16) occur only to the east of the Great Plains; one (*D. arguta*) grows only to the west; some (*D. expansa, D. filix-mas*) (Figs. 6, 3) grow to the east and west, while others (*D. fragrans, D. cristata, D. carthusiana*) (Figs. 1, 18, 19) are continuous across much of North America with the central parts of their ranges however occupying only areas north of the Great Plains. These continuous populations may have been retained through the Pleistocene epoch or perhaps separated populations from the east and west converged and rejoined as the glacier retreated. The main source of North American Woodfern diversity was perhaps eastern Asia. Some taxa probably migrated across land at higher latitudes into the New World during the Tertiary or during interglacial periods of the Pleistocene.

Only two sexual taxa have been derived from tropical America. These primarly Mexican species barely extend into the southwestern United States. They are *Dryopteris patula* (Sw.) Und. var. *rossii*, a diploid of sheltered cliffs in southern Arizona (Kearny & Peebles, 1951), and *D. cinnamomea* C. Chr., found in a cave in Val Verde County, Texas (Reeves, 1978) the chromosomes of which are unreported.

Five of the 15 sexual Woodfern taxa in North America have circumboreal (circumpolar or amphioceanic) affinities while several others have Cordilleran and (or) Appalachian affinities with closely related counterparts in eastern Asia
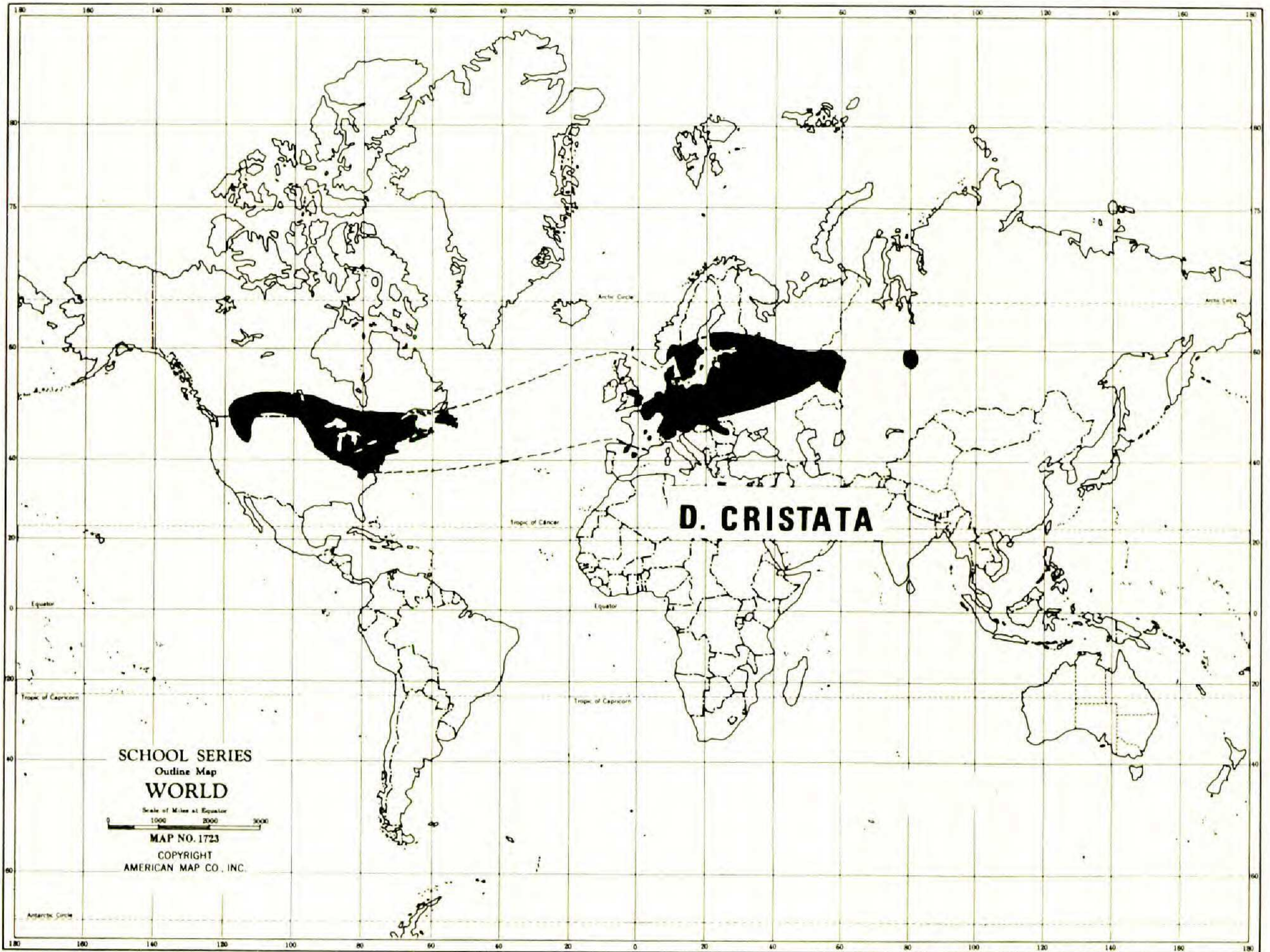
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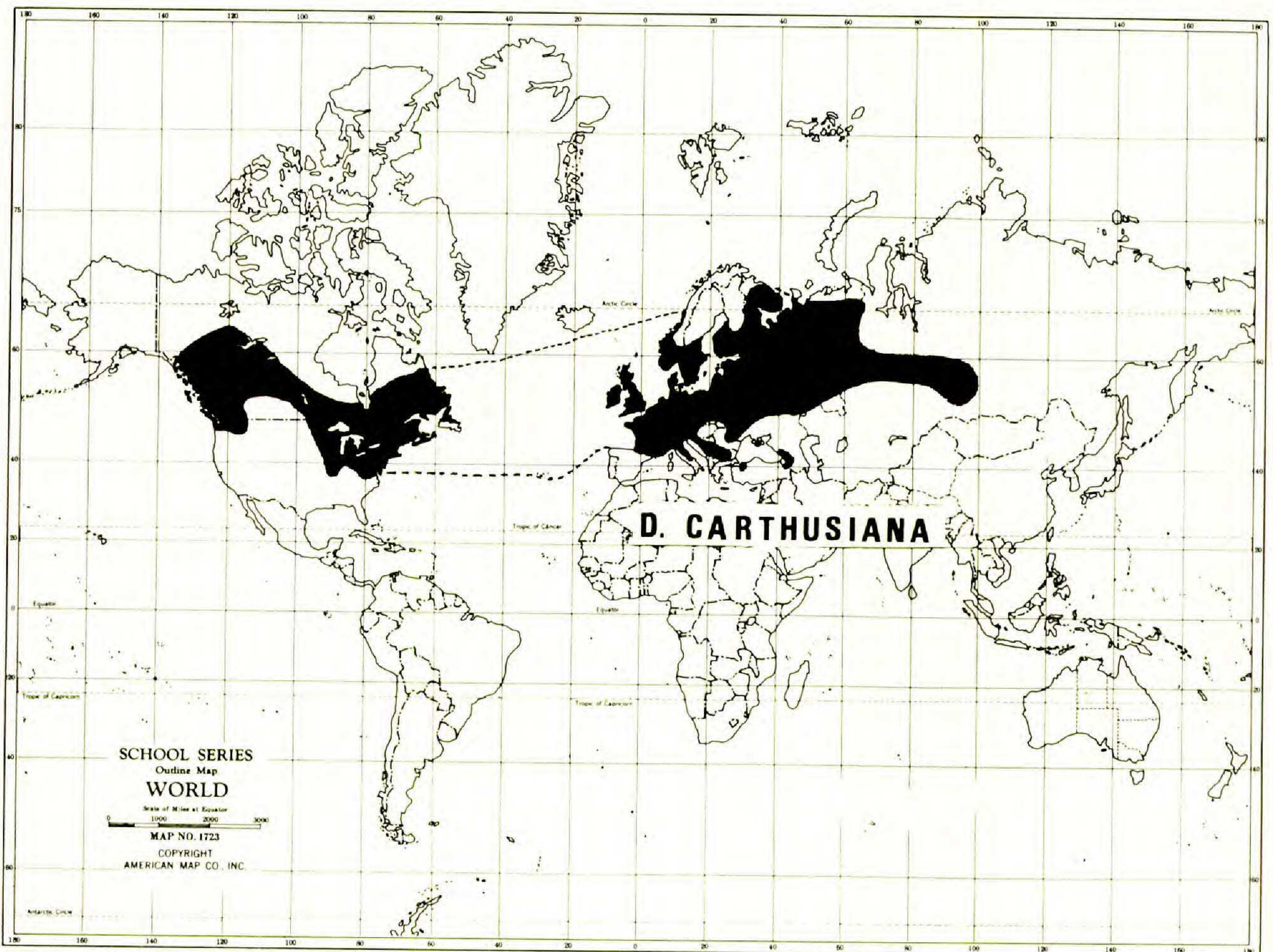FIG. 20. *Dryopteris cristata* approximate global range.

FIG. 21. *Dryopteris carthusiana* approximate global range.

and (or) in Europe. A. C. Jermy (*in litt.*, 1979) suggests that *D. arguta* may be closely related to the Old World *D. villarii (rigida)-D. pallida* complex of Europe and Asia.

Such vicarious affinities suggest that this western North American range may be a relic of a once widespread arctotertiary distribution. Other eastern North American Woodferns that may have Old World vicarious affinities will be discussed below. Many of these may have had ancestral arctotertiary ranges of which only isolated relicts at lower latitudes exist today. During the Pleistocene epoch fluctuating climatic and geologic conditions altered ranges in northern latitudes.

The distributions of the five North American allopolyploids will be analyzed in respect to the ranges of their respective parents. Since the present ranges of the parents of *D. celsa* (*D. goldiana*, and *D. ludoviciana*) (Figs. 12, 11, 10) do not overlap (Wagner & Wagner, 1965), it seems likely that during the advances and retreats of the ice sheet the two ranges conjoined and hybrids were formed which went through polyploidization to form the fertile allotetraploid, *D. celsa*. When the ice sheet finally retreated *D. goldiana* migrated northward separating from *D. lucoviciana*, and the newly formed *D. celsa* established a range (Fig. 12, 13) that is latitudinally and altitudinally intermediate between those of its parents (Wagner, 1971).

Dryopteris clintoniana (Fig. 14) probably resulted from the many disturbed habitats left by the glacier. These habitats allowed for its parents (*D. cristata* and *D. goldiana*) to become established in close proximity as their ranges followed the retreating ice sheet northward (Wagner, 1971). Hybrids formed which underwent polyploidization to form *D. clintoniana*. Its distribution is latitudinally intermediate between and narrower than its parents (Figs. 10, 14, 15, 18), restricted to land covered by deposits of glacial till. The southern border of its range faithfully follows the southern boundary of the ice sheet advance. The fern's localization on glacial till may be a major factor limiting the expansion of its range to the south or north.

The parents of *D. campyloptera*, *D. expansa* and *D. intermedia*, overlap in the northern Great Lakes, southwest Quebec, in the Gaspe Peninsula, Anticosti Island, north of Anticosti Island on the southern coast of eastern Quebec, and west of the Gaspe Peninsula on the northwest shore of the St. Lawrence River, and in the Saguenay River Valley. However, the primarily Appalachian distribution of *D. campyloptera* (Fig. 14) does not directly reflect these areas of overlap (Fig. 15). We suspect that several times during advances of the ice sheet the two parents mingled to a much greater extent as a result of the southward extension of their ranges. Hybrids between them went through chromosome doubling to produce *D. campyloptera* which then followed the retreating glacier northward and developed its present range, the boundaries of which are more northern than those of *D. intermedia* but much more southern than those of *D. expansa*. While *D. campyloptera* may occur in low woodlands in the north, it grows southward almost exclusively in high mountain forests. This supports findings (e.g., Beaman et al., 1962; Reese, 1961a) that suggest that some polyploids are better equipped than their diploid ancestors to inhabit extreme environments at higher altitudes.

The two circumboreal (more specifically amphioceanic) allotetraploid species, *Dryopteris cristata* and *D. carthusiana* form a natural pair. Wagner (1971) suggested that these tetraploids have a common parent ("*D. semicristata*") that possessed a hypothetical SS genome and is now presumably extinct. Among the similarities between these two ferns are leaves partially deciduous, triangular basal pinnae, and preference for moist, acidic lowland habitats. Perhaps the greatest similarity is in their ranges (Figs. 18–21), although a noticeable difference is the more northerly range of *D. carthusiana*. This is not surprising since

the extant putative parent (*D. intermedia*, Fig. 8) of the former has a greater northern distribution than that of *D. ludoviciana* (Fig. 11) the parent of the latter. Since the range of each allopolyploid and one of its parents is known, the approximate range of the hypothetical missing parent, "*D. semicristata*" can be estimated.

Stebbins (1950) stated that there is a tendency for angiosperm polyploids to be more widely distributed than their diploid ancestors. This assumption is evidently not true in several primary temperate fern polyploid complexes. Hirabayashi (1974) found that distribution of the tetraploid Japanese *Dryopteris* are narrower than those of their diploid ancestors. Of temperate North American pteridophyte complexes, twelve examples were taken from the literature (Wagner, 1965, 1966; Wagner and Wagner, 1965; Smith, 1971) and from the results presented above in the present paper. Of them, most have narrower ranges than either of their parents while the rest have a distribution similar to one parent but narrower than the other. While these patterns hold true for most allopolyploid pteridophytes that have been studied, some do have ranges larger than one or both parents. For example, the areas of *D. cristata* (Figs. 18, 20) and *D. carthusiana* (Figs. 19, 21) are both larger than the existing ranges of the presumed extant parents (Figs. 8, 11), but mainly in an east-west direction. If these allopolypoids are very old the original relationship between their range and those of their parents may have become distorted and the patterns no longer evident. Genetic divergence of old polyploids probably slows down considerably and thus acts to conserve primitive ecological and distributional features while related diploids have undergone change (Ehrendorfer, 1980). Since the known parent of each, *D. intermedia* and *D. ludoviciana*, are diploids, their ranges may have shifted more than those of the allopolyploids. Their parental diploids may even have had world-wide distributions in the past. To understand the original relationships between the ranges of allopolyploids and those of their parents, the most revealing studies may be on what we assume to be fairly recently developed allopolyploids (e.g., *D. campyloptera*, *D. celsa*, and *D. clintoniana*). The generalized relationship between the ranges of allopolyploid pteridophytes and those of their parents has been summarized as follows (Wagner 1969): "Of the hybrid pteridophytes . . . those which are not entirely sympatric with the parents show less east-west correlation with the parental ranges than north-south. The north-south distribution is intermediate as we might expect." No matter what size the range of an allopolyploid pteridophyte is in relation to those of its parents, latitudinal intermediacy between them can usually be anticipated. Therefore, we expect that if "*D. semicristata*" were present today it would grow approximately within 50°–80° N latitude and possibly have a circumpolar distribution.

If we assume that *Dryopteris ludoviciana* is the other parent of *D. cristata* in addition to "*D. semicristata*," then the origin of *D. cristata* must have occurred in the New World. However, a native Asian diploid fern, *D. tokyoensis* (Mak.) C. Chr., with the same chromosome number as *D. ludoviciana* ($2N = 82$) grows in Japan, Korea, and parts of China in only slightly higher latitudes than *D. ludoviciana* and in a similar climate. (A similar vicariant relationship exists between *D. goldiana* of eastern North America and *D. monticola* C. Chr. of Japan which are morphologically similar.) *D. ludoviciana* (Fig. 22A) and *D. tokyoensis* (Fig. 22B) are similar morphologically, but the former has fronds which are slightly more dissected and pinnae which are more dimorphic than the latter. Perhaps they have a common ancestor that had a worldwide range that through time became fragmented, and geographical separation of the populations diverged into vicarious species. Where the ancestral range overlapped with that of "*D. semicristata*" in the northwestern and north central Old World, hybrids may have formed that underwent chromosome doubling to produce *D. cristata*, which eventually developed a circumboreal distribution. When the Pleistocene con-
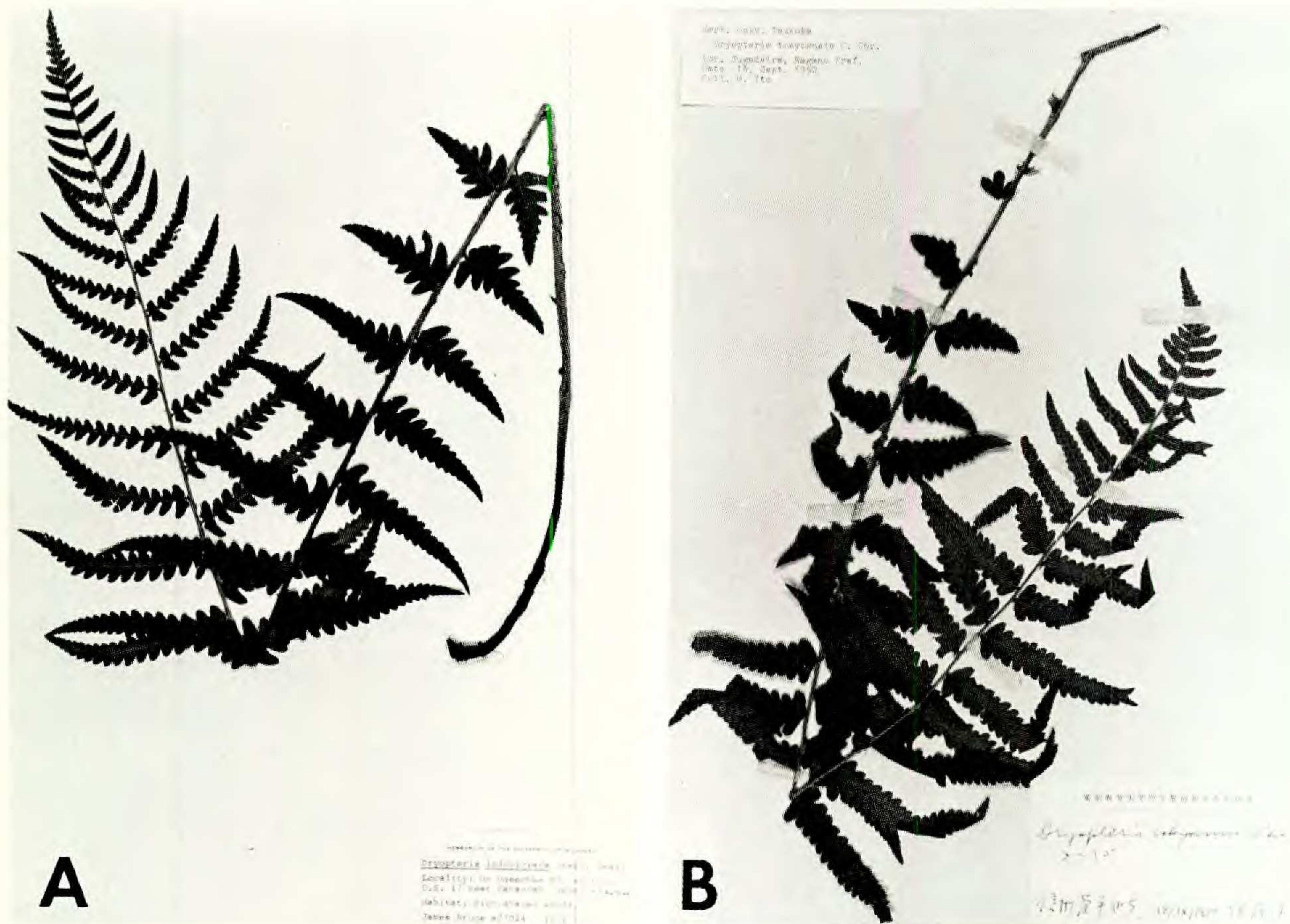
FIG. 22. Frond A is *Dryopteris ludoviciana*. Frond B is *Dryopteris tokyoensis*.

tinental ice sheet extended southward, all the populations of the circumpolar "D. semicristata" were presumably eradicated by the advancing ice. The present eastern Asian range of *D. tokyoensis* may be a fragment of a former broad Old World range that survived the glaciation. The ability of *D. cristata* to survive the extreme conditions produced by glaciation more successfully than its diploid parents may be explained by suggestions (e.g., Stebbins, 1950; Reese, 1958, 1961a) that polyploids are better equipped than their diploid ancestors to adapt to extreme conditions since they have more alleles and therefore greater genetic flexibility. Hence the origin of *D. cristata* may have been in either the Old or the New World or possibly in both hemispheres.

Assuming that *Dryopteris intermedia* is the other parent of *D. carthusiana* in addition to "*D. semicristata*," the origin of *D. carthusiana* may also have been in the New World. However, the Old World species, *D. madierensis* Alston and *D. azorica* (Christ) Alston, apparently possesses the same basic genome as the *D. intermedia* (Gibby, 1977; Gibby and Walker, 1977) and the three comprise a species aggregate. These findings were determined by chemical (Widén & Britton, 1969; Widén et al., 1970; Widén, Britton et al., 1975; Widén, Lounasmaa et al., 1975), cytological (Gibby & Walker, 1977) and morphological (Walker, 1961) comparisons. One difference that exists between them is that the Old World representatives do not possess the epidermal glands so characteristic of the New World *D. intermedia*. This lack of glands is important since *D. carthusiana* is glabrous or nearly so. If the glandular New World *D. intermedia* were a parent of *D. carthusiana* one would expect to find more glands on *D. carthusiana* since they are present on other North American Woodfern hybrids involving *D. intermedia*. Since *D. carthusiana* is glabrous or nearly so we suspect the existing glandular New World *D. intermedia* is not a likely immediate parent, although a glabrous New World ancestor may have been a parent of *D. carthusiana*. Presently there exist nearly glabrous populations of *D. intermedia* in the southern part of its range in the Appalachian mountains of North Carolina (Wagner, unpublished).

These "glabrous" populations are probably primitive judging from outgroup comparison with its relatives and indicate that the ancestor of the glandular *D. intermedia* was glabrous. Under these circumstances *D. carthusiana* could have originated in the New World. An Old World origin of *D. cathusiana* is, however, equally possible, even though presently *D. madierensis* is only known on the continental island, Madeira Island (450 miles from Morocco) while *D. azorica* is only known on the oceanic islands, the Azores (900 miles from Portugal). Most taxa on island floras are the same as, or related to, widely distributed continental species. The dominance of widely distributed species in island fern floras clearly reflects an ability to migrate from continents. Their proportion on islands are much higher than their proportions in source areas (Tryon, 1970). Page (1973) concluded that the Canary Island (50 miles from Cape Yubi, Africa) fern flora is largely made up of ancient species that existed in Tertiary Europe, and have survived, little changed, as relics in the island mountains. Studies on Madeira Island (I. Manton, J. D. Lovis and G. Vida, unpublished; I. Manton et al., unpublished; as cited in Lovis, 1977) have also yielded evidence that these islands may have provided refugia for forms that are no longer capable of surviving elsewhere. Accordingly the insular *D. azorica* and *D. madierensis* may actually be remnants of an ancestral range which extended through northern Africa into western and central Europe in mid-Tertiary times. Where the ancestor overlapped that of "*D. semicristata*," hybrids formed that doubled to produce *D. carthusiana* which eventually developed its circumboreal distribution. Gibby (1977) suggested that *D. madierensis* or *D. azorica* may have occurred together with *D. expansa* in the past in Europe to give rise to the allotetraploid *D. dilatata* (s. str.), which has a similar genome, and may be conspecific with the North American *D. campyloptera*. When the Pleistocene ice sheet extended southward, the entire continental range(s) of *D. madierensis* and *D. azorica* or their ancestor may have been destroyed along with that of "*D. semicristata*." These island populations survived the Pleistocene glaciation because of a buffered island habitat. The continental range of *D. carthusiana* was able to survive glaciation for the same reason mentioned above for *D. cristata*. Hence, the origin of *D. carthusiana* may also have been either in the Old World or the New World or possibly in both hemispheres independently.

In the modern arctic climate, habitat instability is still an outstanding feature, and it is likely that new polyploid races are being produced where opportunities for hybridization and successful establishment of new genotypes obtain (Johnson, Packer & Reese, 1965).

The frequency of polyploids in areas that were altered by climatic conditions of the Pleistocene epoch suggests that these environments were outside the tolerance limits of many of the existing diploid species and that they were invaded by older polyploids (e.g., *D. cristata* and *D. carthusiana*) as well as by the proliferation of new variable hybrid polyploids (e.g., *D. campyloptera*, *D. celsa* and *D. clintoniana*.)

SUMMARY

The 15 sexual taxa of Woodferns (*Dryopteris*) living in North America north of Mexico, display a diverse array of geographical ranges that correlate with topography, climate, past glacial activity, habitat availability. The ranges bear upon possible phylogenetic origins. Two diploids, *D. fragrans* and *D. expansa* and the tetraploid, *D. filax-mas* all have circumboreal distributions. The western *D. arguta* extends mainly through Pacific coastal ranges while *D. cinnamonea* and *D. patula* var. *rossii* reach their northern limits in southern United States. Four diploid species (*D. goldiana*, *D. intermedia*, *D. marginalis* and *D. ludoviciana*) grow exclusively in eastern North America. All of these occur from Canada south

through the Appalachians to the upper fringes of the southeastern United States coastal plains except *D. ludoviciana,* which is restricted wholly to the southeastern United States coastal plain. The other Woodferns that grow exclusively in eastern North America are fertile allopolyploids: *D. campyloptera,* mainly of northern and middle latitudes in the mountains; *D. clintoniana,* of middle latitudes; and *D. celsa,* of middle and southern latitudes. Pleistocene glaciation probaby influenced the origins of these allopolyploids by forcing co-habitation of their respective parents in response to advancement and retreat of the ice sheet. The final two North American Woodfern species (*D. cristata* and *D. carthusiana*) are both circumboreal allopolyploids. It has been suggested that they may have a common parent (SS genome) now presumably extinct. Strong similarities between the ranges of these two allotetraploids support this suggestion. Their origin may have been either in the Old World or the New World or possibly in both hemispheres.

ACKNOWLEDGMENTS

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